INSECT TRANSMISSION

OF

PLANT DISEASES

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A honey bee collecting nectar from an apple blossom One of the first insects to be incriminated by experimental evidence as vectors of a plant pathogen   The blight bacteria grow in the nectar and multiply there are saprophytes and then enter the tissues   The Bacillus of blight in the nectar is carried from flower to flower by insects visiting the flowers for pollen and honey   An artificial epidemic of pear blight started by infecting a few trees on the edge of an orchard and allowing free access of insects   Mosquito net bags over the flowers kept out insects therefore protect the flowers from blight "   (*Waite* 1891)

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PLANT DISEASES

BY

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DEDICATED

TO THE MEMORY OF

ROYAL N CHAPMAN

PREFACE

During the past twenty-five or thirty years, there has appeared in the literature of plant pathology a constantly increasing amount of evidence that insects play an important role in the spread and development of many plant diseases. Much of this evidence has never been adequately summarized or coordinated and is to be found only in widely scattered publications. In this book, the author has endeavored to bring together in one publication the most important contributions in this field of study. An effort has been made to evaluate and interpret the evidence in the light of the more recent advances in entomology and plant pathology.

Because the author feels that the subject has not received sufficient attention from teachers and research workers, he has presented it in a manner that frankly strives to emphasize the importance and promise of the subject as a field of study and research. The book is published, therefore, with the hope that it will stimulate greater interest in the subject among those students who are concerned with the problems of plant protection.

In presenting the material, an effort has been made to be brief. No attempt has been made to discuss all diseases transmitted by insects or all insects that transmit diseases. Emphasis has been placed on those which have been investigated most completely or which are best suited for illustrating the various principles of insect transmission. Moreover, in discussing a disease only those facts relevant to insect transmission have been included. Much information of general interest in plant pathology has been omitted purposely. In most cases, however, suitable references to such information have been given. In like manner, no complete technical descriptions of the insect vectors have been included. This information can be obtained readily from standard entomological texts or from the special references cited.

Because of the method of presentation, in which certain chapters deal with specific examples of insect transmission and

others with the principles involved, a small amount of repetition has been unavoidable It is believed however, that the added convenience to readers with different backgrounds of information will more than compensate for any objectionable features of this method of arrangement

The author first became impressed with the potentialities of this field of study in 1923 when an investigation of the blackleg disease of potatoes led him into a study of the role of Dipterous insects in the spread and development of the bacterial soft rot of plants Since that time, he has actively prosecuted research in some aspect of the association of insects with plant diseases From 1932 to 1938 he taught a course in the subject in cooperation with Prof A A Granovsky of the Department of Entomology and Economic Zoology at the University of Minnesota A similar course is now taught by the author at West Virginia University

The idea of writing such a book was originally suggested in 1929 by the late Dr Royal N Chapman, whose interest and enthusiasm caused the author to continue his activity in this field of study Without Dr Chapman's constant encouragement, the book would not have been written The preparation of the manuscript was begun while the author was professor of plant pathology at the University of Minnesota and has been completed at West Virginia University The author is indebted to his colleagues at both institutions for aid in many different ways He is grateful to Dean E M Freeman for much helpful advice and encouragement Thanks are expressed to Drs Clyde Christensen Carl J Eide, E C Stakman, Leon H Leonian and Carlton F Taylor for critically reading the entire manuscript and to Dr Clarence A Mickel for reading Chap XIII and for aid in determining the correct names for a number of insects Many helpful suggestions have been received from these colleagues, but the author assumes full responsibility for any errors in the text Acknowledgment is due also to Dr A A Granovsky, who was associated with the author in the course offered at the University of Minnesota, for reading the first draft of Chaps I to VI

The author is grateful indeed to those who have kindly furnished illustrative material specific acknowledgment of which is given elsewhere The illustrations not otherwise designated

are from the files of the Department of Plant Pathology of the University of Minnesota or the Department of Plant Pathology and Bacteriology, West Virginia University

The references cited, with the exception of about 30 titles have been checked for accuracy with the card catalogues of the Library of the U S Department of Agriculture or with originals deposited there Grateful appreciation is expressed to the Bureau of Plant Industry Library staff for making these facilities available

<div align="right">JULIAN GILBERT LEACH</div>

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INSECT TRANSMISSION OF PLANT DISEASES

CHAPTER I

INTRODUCTION

Since the dawn of civilization, man has been interested in the
health of plants   In all probability plants were subject to
disease long before they were brought under cultivation, but the
diseases were of little concern to man until he began to give
special care to those plants that furnished him food   At first
the diseases were attributed to supernatural phenomena, and
their control was sought only through appeasement of the
appropriate gods   With the development of more intensive
agriculture through the ages, the necessity of protecting crop
plants against disease has become progressively more acute, and
consequently a more scientific attitude toward the problem has
developed

For many centuries, however the study of plant diseases was
dominated by dogma and superstition for the nature of diseases
remained obscure and little or nothing was known of micro-
organisms   In later years when microorganisms were observed
to be associated with diseased plants they were interpreted, at
first, as products rather than as causes of the abnormal conditions
It was not until the middle of the nineteenth century, when the
classical studies of De Bary definitely established the pathogenic
nature of certain fungi, that the subject was placed upon a true
scientific basis   With this new concept of the nature of plant
diseases, progress was relatively rapid and much was learned
about the diseases of plants and how to control them   Naturally,
however, emphasis was placed on the etiological aspect of the
diseases and for many years the more important works were
descriptive in nature   Thought was dominated almost com-
pletely by the mycological viewpoint   This influence is still

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very strong, and, even now, there are some who look upon phytopathology as nothing more than applied mycology   Much of the research in contemporary plant pathology is still descriptive and exploratory   Only in very recent years has attention been given to other and more fundamental aspects of the subject

Even control measures, to a large extent, have been based on empirical studies with only a superficial understanding of the many factors involved   Spray programs and seed treatment practices, for the most part, are based upon incomplete data obtained empirically, and relatively little is known of the nature of the action of the fungicides or the factors that influence their effectiveness   Satisfactory control of plant diseases cannot be achieved until we know much more than we do now about their nature and the factors that influence their development

A Neglected Borderline Field —There is no aspect of the study of plant pathology more fundamentally important than that dealing with the methods by which diseases are transmitted and the relative significance of each method   Successful control measures, with few exceptions, are dependent upon a knowledge of these facts   Yet the subject has received only casual treatment, and the facts of transmission are known thoroughly for only a relatively small number of diseases   The role of insects in the spread and development of plant diseases has been especially slow in receiving the attention that it deserves   Plant pathologists have been inclined either to avoid a study of insects associated with diseases or to treat the problem in a very superficial manner   This attitude has resulted in the neglect of a field of study that is very important in phytopathological research

The problem has been neglected to an equal degree by the entomologists   Economic entomology, like phytopathology, is relatively young, and workers in this field also, until quite recently have been engaged in the descriptive aspects of their science   They have been so greatly concerned with the direct injury to plants by insects that they have had very little time for the study of the more obscure injury caused by insects acting as vectors of plant diseases   It is safe to say that the subject of insects in their relation to plant diseases has received no more attention from the economic entomologist than it has from the phytopathologist

Phytopathology and economic entomology have one large problem in common, namely, the problem of plant protection Workers in both fields are concerned with protecting our agricultural crops against those innumerable pests which take such a large annual toll from the farm income In spite of this common interest in a problem of such vital importance to human welfare, the two sciences have widely divergent viewpoints These different viewpoints can be explained partly by the origin of the two branches of science Only a few generations ago, biology was considered a highly specialized subject, and it was possible for one man to obtain a fair mastery of the entire field As science progressed, the sum total of biological knowledge increased so rapidly that one man no longer could master the whole field Specialization and division of labor became necessary The first division separated biology into botany and zoology With the continued rapid growth of science, each of these has since been divided and subdivided into a bewildering number of branches, each branch having its own technique and vocabulary

Phytopathology is essentially a botanical science whereas economic entomology is a zoological science Today two young students of biology start out together but very soon they come to the parting of the ways, one traveling the road of a zoologist, the other that of a botanist After years of training one becomes a plant pathologist, the other becomes an economic entomologist, and they meet again, faced with the common problem of plant protection They both realize the necessity of working together and attempt to cooperate, but unfortunately 'they don't speak the same language '' In the course of their training their viewpoints have become too widely separated and too greatly specialized

This situation has resulted in the neglect of a large field of information that is vital to the solution of many problems of plant protection As the two sciences have advanced steadily, there has been left behind a large ''no man's land' in which are many unsolved riddles and unanswered questions One of the most important of these neglected borderline problems is that of the relation of insects to the spread and development of plant diseases

Nearly fifty years ago, Waite (1891) first established the fact that insects were of significance as vectors of plant diseases by

demonstrating that fire blight of pears is transmitted by bees
At approximately the same time, it was discovered that insects
and other arthropods were of very great importance as vectors of
diseases of man and other animals   Yet despite the significance
of these early discoveries, progress in the study of insect trans-
mission of plant diseases has been relatively slow   The plant
pathologist with his vague knowledge of insects has found it too
easy, when faced with an insect-disease complex, to shirk his
responsibility by saying, "That's up to the entomologist "   In
a similar manner, the entomologist has found it equally easy to
avoid any problem that might involve a mycological or bacterio-
logical study   It is obvious to one familiar with the phytopatho-
logical and entomological literature that this attitude often has
delayed for many years the discovery of important facts of
insect-plant disease relationships   For the purpose of illustra-
tion it may be well to mention a few examples

The seed-corn maggot has been studied extensively by ento-
mologists who were well aware of its association with decayed
plant tissue, but until recently the insect has been considered as
a scavenger attacking only decayed plants (Schoene 1916)   In
spite of the almost constant association of the insect with potato
plants affected with bacterial soft rot, it was completely ignored
for many years by all plant pathologists who studied the disease
The failure to recognize the significance of the association can
be attributed largely to the prevalence of the idea that the insect
lived entirely as a scavenger   It was only when the insect and
the bacterial disease were studied together that the true relation-
ship was discovered (Leach 1926)

The bacterial wilt of corn has been studied by plant pathol-
ogists since 1897   Early work led to the incorrect conclusion
that it was entirely seed-transmitted   Its true methods of
transmission were not known until quite recently   Long before
it was discovered that the disease is transmitted by the corn flea
beetle the injury caused by this insect was described by ento-
mologists in terms that leave no doubt of the fact that bacterial
wilt was present but unrecognized   Forbes (1905), describing
the injury to sweet corn caused by the flea beetle in 1891, stated
that "whole fields were wilted more or less and some hills entirely
killed '   This striking injury was attributed to the insect alone
without mention of a disease   Metcalf and Flint in 1928

described flea-beetle injury as follows "The green portion of the leaf is eaten, giving the whole plant a bleached appearance, growth is retarded, and the leaves wilt even during wet weather " Every plant pathologist will recognize this as a good description of the symptoms of bacterial wilt

The destructive hopperburn of potatoes was confused for many years with tipburn and attributed entirely to the effects of excessive transpiration   In 1918 Ball showed that the greater part of the injury attributed to "tipburn ' was caused by the feeding activities of the leaf hopper (*Empoasca fabae* Harris) Had plant pathologists who studied the condition been less reticent in observing the insects the true cause probably would have been discovered sooner

The fungi causing blue stain of coniferous wood have been studied by forest pathologists for many years but it was not until 1929 that these fungi were shown to be pathogenic to living trees   Although their association with the bark beetles had been observed, the significance of the bark beetles as vectors of the fungus was not discovered until an entomologist questioned the ability of the beetles alone to kill the trees so rapidly (Craighead 1928)   Work done in response to this question showed that the death of the trees was caused primarily by the blue stain fungus introduced into the sapwood by the bark beetles (Nelson and Beal 1929)

The Need for Cooperative Effort —The discovery of the nature of virus diseases of plants and the role of insects in the transmission of viruses has greatly stimulated the interest of both entomologist and pathologist in the general subject of insect transmission of plant diseases   The appearance in Europe and America of the destructive and spectacular Dutch elm disease, which is so dependent upon insects for its spread and development, also served to focus the attention of both groups of workers on the problem   The necessity for cooperation between entomologist and plant pathologist in the solution of these borderline problems is now generally recognized by both groups, and the need has been expressed in the literature on numerous occasions For various reasons, however, the present situation leaves much to be desired   It is one thing to talk of cooperation and another thing to cooperate   In fact, so much has been said and written in recent years about cooperation in research that the word, to

some extent, has fallen into disrepute   Cooperation often works much better on paper than in practice   In order to avoid the difficulties of cooperation, we often plead for coordination of effort   This sounds much better but is often more difficult, for it requires a great deal of earnest cooperation before we can have successful coordination   But despite all these difficulties there is, and has been, a fair amount of real and successful cooperation in scientific research

The failure or lack of cooperation may be caused by many different factors   The human or personal element is perhaps the most common of them all and the most difficult to overcome   Other causes may be administrative, political or, as indicated above, largely a matter of tradition   However, it is the author's belief that the greatest success in the solution of borderline problems cannot be achieved by the expedient of cooperation alone   Cooperative work is sometimes attempted on the principle of strict division of labor in which all "entomological" work is done by the entomologist and all "phytopathological" work by the phytopathologist   This type of cooperation nearly always is doomed to failure   In the study of the relation of insects to plant diseases, such strict division of labor is not practical   For the greatest success, the invisible, though very real, wall separating the two fields of research must be broken down   This may be rather difficult, but it can be done

A first step in this direction would be a liberalization of the narrow professional viewpoint, which in effect often hangs out a sign reading, ' This is the phytopathological field, entomologists encroach at their own risk" or "This is the entomological field, all phytopathologists keep off "   Such a viewpoint may simplify some of the problems of organization, but it is not conducive to the solution of these neglected, but mutually important problems   The necessity for well-defined fields of research with corresponding responsibility and authority is recognized   Such responsibility and authority are necessary, not only for efficient administration, but also for the existence of the guild spirit so important in scientific research   Nevertheless, when attempts are made to draw too sharp a line between related fields of activity many problems of vital importance and significance usually are neglected

A second step would be a modification of our educational procedure so that research workers would be given the viewpoint and training in techniques necessary for the solution of the problem in hand. The worker should have a thorough knowledge of the essentials of both entomological and microbiological techniques. Instead of placing the emphasis upon training entomologists or plant pathologists, some of the workers should be given the training and viewpoint necessary for the solution of this particular kind of problem, namely, the role of insects in the spread and development of plant diseases. It is not proposed that we train mental giants who can master both fields of knowledge, but rather workers who have a sufficient grasp of the essentials of both sciences for the solution of this particular kind of problem. When these qualifications are combined in one man, many of the difficulties of cooperation will be avoided. No claim is made for the novelty of the idea, for already it has met with considerable success in the solution of other borderline problems.

The Complex Nature of the Problem —The problem of insects in relation to plant diseases is by no means a narrow and restricted field. It includes the study of many questions of broad biologic significance. Insects and plants, including microorganisms, have been closely associated throughout their evolutionary history. In the course of their evolutionary development many different types of insect-plant associations, with varying degrees of complexity, have arisen. Some of these have a direct and fundamental bearing on the problem of disease transmission. For example, the phenomenon of entomophily or insect pollination of flowering plants, is a biologic association that has much in common with the insect dissemination of plant pathogens. The two associations are strikingly similar in many respects. A student of insect transmission of plant disease will find much of stimulating interest in a study of insect pollination of flowering plants. Similarly, the subject of symbiosis between insects and microorganisms is of vital interest to anyone concerned with the study of insect transmission of plant diseases. There are numerous examples of insect transmission of plant pathogens in which there is a condition of mutualistic symbiosis between the pathogen and its insect vector. For every known association between

insect and pathogenic microorganism, there are numerous similar associations between insects and nonpathogenic microorganisms The fundamental biological principles are usually the same in both cases For these reasons, the whole category of interrelationships between plants and insects is considered fundamentally significant to a proper study of the problem of insect transmission of plant diseases The association of insects with plant pathogens is only one of several such relationships A perspective of the entire group of insect-plant associations is essential to the best understanding of any particular one

When insects are concerned in the transmission of a plant disease, three organisms often are involved the plant (the suscept), the pathogen, and the insect vector The association may be, and usually is, more complex than one would conclude from a casual study For a thorough understanding of the association, the morphology and physiology of all three organisms must be reasonably well understood Under our present plan of graduate study, very few students of either phytopathology or entomology are sufficiently well grounded in the subjects of plant anatomy, plant physiology, microbiology, insect morphology, and insect physiology to understand clearly the significant biologic processes involved in such an association Moreover, simple morphological and physiological processes often take on entirely new aspects when involved in such a three-way association

It is a principle well recognized in plant pathology that, in the study of the epiphytology of a plant disease, one must consider the influence of the environment not only on the suscept and on the pathogen but also on the interaction of the two When a third living organism the insect vector, is introduced, the ecological relations are complicated to a surprising degree, and new kinds of problem arise The ecological aspect of insect-transmitted plant diseases is a field of investigation that is yet to be exploited extensively This phase of the insect-transmission problem has been studied more completely in connection with the curly top of sugar beet than any other disease A study of the ecology of the vegetation on weedy, abandoned farm lands and the problem of overgrazing are subjects that would have had very little interest for plant pathologists in the earlier studies of curly top Because of their relation to the insect vector of the disease, these studies are now important aspects of the curly-top

investigations A different type of ecological study is represented also by the work of Fife and Frampton (1936) They showed that the pH gradient from the phloem to the parenchyma of the beet leaf is a factor determining the tissues fed upon by the leaf hoppers This ecological study has thrown much light on the problem of insect transmission of curly top and may help explain the high degree of specificity often found in insect transmission of viruses

The study of the more detailed relationships between insect vectors and the diseases transmitted by them includes many problems, the solution of which is definitely limited by the lack of satisfactory techniques No science can advance more rapidly than the techniques available for its study The desired technique may be a combination of methods peculiar to microbiology and entomology or something entirely new These problems of technique offer unique opportunities for those workers who approach them with the proper background of training and experience

The discovery that insects are concerned in the transmission of plant diseases was made at approximately the same time that it was demonstrated that insects could transmit diseases of man and other animals, but study of the subject has progressed somewhat more rapidly in the field of animal pathology than it has in plant pathology This difference may be explained in part by the greater value placed upon the life and health of man and his domesticated animals as compared with that of plants However, the principles involved in insect transmission of the two groups of diseases in so far as they are comparable, are strikingly similar The student of insect transmission of plant diseases can learn much from a study of the known facts about insects as they are concerned in the spread or the diseases of man and other animals

The importance of insects in the transmission of the diseases of man has lead an increasingly large number of investigators into this field of research These investigators are trained in the fundamentals of both entomology and medical science They have for their goal the solution of a particular kind of problem, namely, the role of insects in the spread and development of diseases of man Their work has contributed much to the remarkable advances in medical science in the past few decades It would

seem that the time is ripe for a similar development in the field of plant pathology

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CHAPTER II

THE INTERRELATIONSHIPS OF PLANTS AND INSECTS

Plants and insects have inhabited the earth together for millions of years During this time, each group has undergone extensive evolution A few relatively simple kinds have given rise to almost innumerable species with a remarkable complexity of form and function The most important factors in determining the course of this evolution have been the intense struggle for existence and the inevitable natural selection Plants and insects have lived in close association under conditions that led to many types and degrees of interdependence Because of the survival value of some of these associations progressive evolution in the direction of greater interdependence has taken place Consequently many diverse and complex interrelationships between plants and insects arose and some of them have survived to the present time

We are interested here primarily in those associations in which the insect is concerned in some way with the spread or development of plant diseases, but a satisfactory discussion of this relationship depends to some extent upon a knowledge of the other kinds of association For this reason, a brief analysis of the various interrelationships of plants and insects is given

The numerous interrelationships of plants and insects may be classified conveniently in the following six groups

1 Insects that feed upon plants (phytophagous insects)
2 Plants that feed upon insects (entomophagous plants)
3 Plants that cause diseases of insects (entomophthorous plants)
4 Plants that are pollinated by insects (entomophilous plants)
5 Insects and plants that live in symbiosis
6 Insects that disseminate plant pathogens or aid in the development of plant diseases

1 PHYTOPHAGOUS INSECTS

This is perhaps the best known and most universal insect-plant relationship Insects, in common with all other forms of animal

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life, are either directly or indirectly dependent upon plants for food   Plants, by virtue of their ability to fix the energy of the sun through the process of photosynthesis, are ultimately the source of the food for all animals   Neither insects nor any other form of animal life could survive if there were no plants   Insects, in feeding upon crop plants, inflict losses amounting to many millions of dollars annually   One needs only to mention such
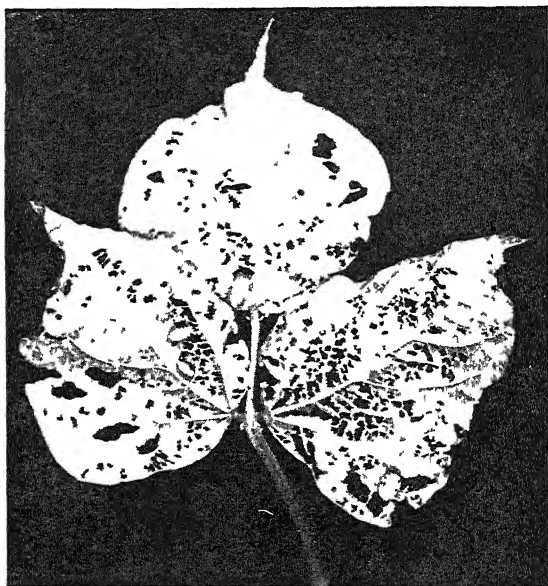
Fig 1 —A typical chewing insect the Mexican bean beetle (*Epilachna corrupta* Mulsant)   Five larvae and one adult bettle feeding on a bean leaf

examples as the grasshopper, the chinch bug, cutworms, and white grubs to picture this aspect of the relationship   Insects feed not only on living plants but also on all types of stored plant product   All kinds of plant from the smallest microorganism to the largest tree are utilized by them   Insects feed in many different ways   Some, such as grasshoppers and beetles, chew the plant tissues and digest them (Fig 1), others, such as aphids, leaf hoppers, and chinch bugs, puncture the plants and suck the sap from the living cells (Fig 2), still others, including bees, wasps, and butterflies feed upon nectar and other plant exudates   Fig 3)   Whatever the method of feeding, the insects are usually

highly specialized for the utilization of some particular kind of plant or plant product
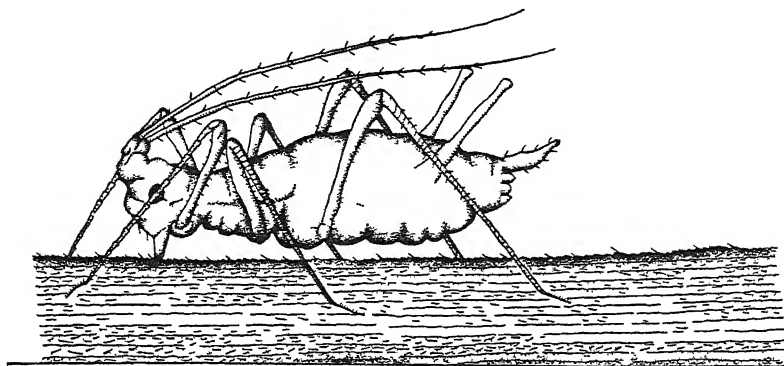
Fig 2 —A sucking insect, an aphid, feeding on the mid-vein of a potato leaf The insect's beak is penetrating deep into the tissues of the plant from which cell sap is being drawn   (*After Houser Guyton, and Loury*)

In addition to the direct destruction of tissue by feeding many phytophagous insects indirectly destroy plants by breeding
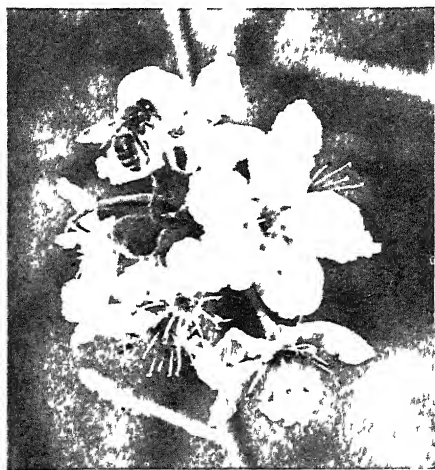
Fig 3 —A honey bee sipping nectar from an apple blossom   A representative of a large group of insects that feed upon plant products without wounding the plant tissues

in the tissues   Some species spend much of their life span boring or mining in some part of the plant and often cause as much

damage in connection with breeding operations as they do by direct feeding (Fig 4)

Some insects are *polyphagous*, feeding upon an almost unlimited number of plant species   Others are *oligophagous*, feeding upon a limited number of closely related plant species   Still others, such as certain species of aphids, are *polyphagous* during one season or one stage of development and *oligophagous* during the others   A few insects restrict their feeding to a single species or variety of plant and are classed as *monophagous*   The number
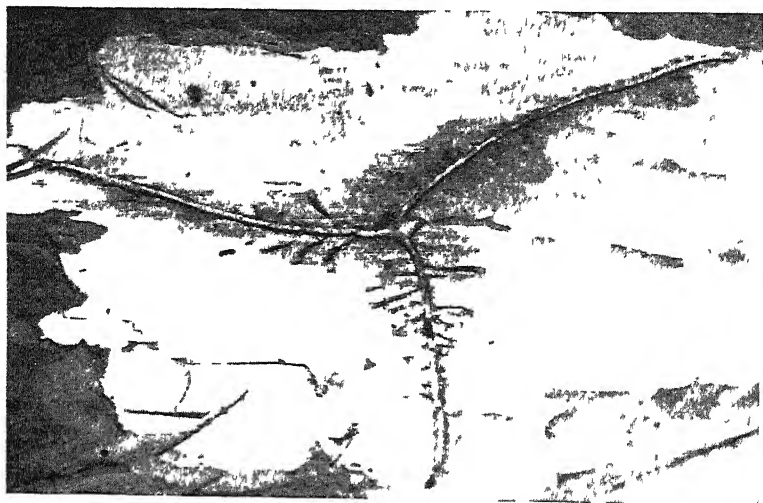
FIG 4 —The brood gallery of the pine bark beetle (*Ips pini*) in the sapwood of a red pine tree

of different insect species that may feed upon a single plant species varies widely   Some plants such as poison ivy [*Rhus toxicodendron* (Tourn) Mill] serve as food for less than half a dozen insect species, whereas others, for example, the oak and apple, are hosts for four or five hundred different species

The injury caused by insects that attack cultivated crop plants is so great that one often overlooks the fact that some insects feed upon and destroy noxious plants   Those feeding upon the various species of cactus (*Opuntia spp*) have rendered notable service in the control of these plants in Australia (Prickly-Pear Land Commission 1925 to 1932)   Several species of *Opuntia* were introduced into Australia about 1840 as ornamental plants

They escaped and multiplied as weeds so rapidly that by 1870 they were out of control Largely because of the absence of natural enemies, they continued to spread until more than 60 million acres of land were made unfit for agricultural purposes The cactus plants, especially those of *Opuntia enermis* and *O stricta*, grew in such dense masses that all ordinary cultural practices were ineffective in preventing their spread The insect enemies of *Opuntia* were then introduced from Texas and Argen-
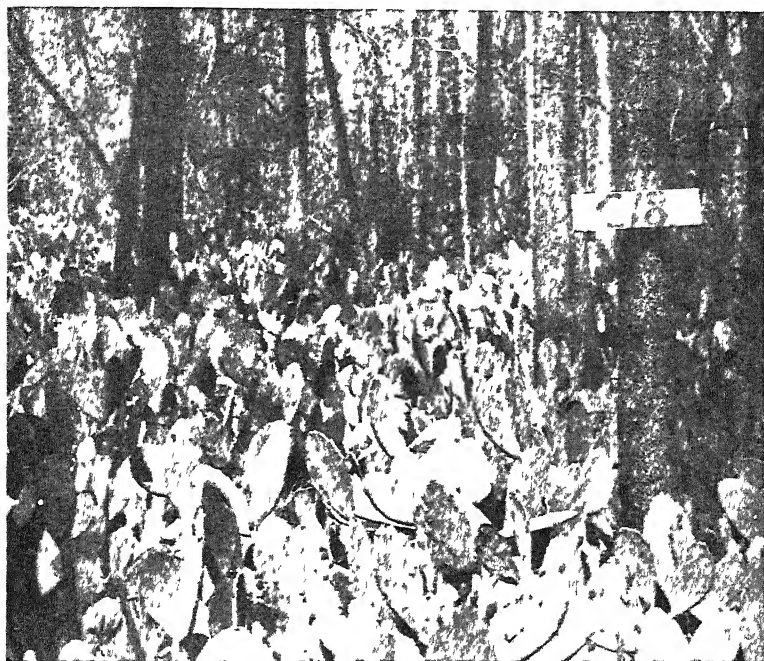
Fig 5 — A dense infestation of prickly pear (*Opuntia inermis* before subjected to the attack of the insect, *Cactoblastis cactorum* Compare with Fig 6 (*After Dodd*)

tina, and they together with the microorganisms that they transmit have been so effective that approximately twenty-five million acres have been reclaimed and further spread of the cactus has been checked (Dodd 1927, 1933 1936) Of the insects introduced, the Argentine moth borer (*Cactoblastis cactorum* Berg) has been by far the most effective (Figs 5 and 6)

This outstanding success of cactus control by insects in Australia has focused the attention of entomologists upon the

influence of insects on the growth of weeds under natural condi-
tions and the possible use of insects in the control of other noxious
weeds   In general, the most noxious weeds are those which
have been imported into a new region where their insect enemies
have not become established   Often they are not considered
noxious in their native habitat, and it is entirely possible that

Fig 6 —The same area of prickly-pear infestation shown in Fig 5 three years
later after infestation with *Cactoblastis cactorum*   The prickly pear plants have
been destroyed by the insect and the microorganisms transmitted by it, insert
adult and larva of *C cactorum*   (*After Dodd*)

their noxious character would be greatly decreased if the insects
and other pests that feed upon them in their native home were
introduced to the new locality   This possibility has been
investigated only superficially but is worthy of further study

Insects are also important scavengers and consume many kinds
of dead plant tissue that would otherwise accumulate in exces-
sive amounts   Ants are said to be of especial importance in this

respect in the tropics Insects and fungi usually are closely associated in the destruction and decomposition of plant remains

2 ENTOMOPHAGOUS PLANTS

A number of plant species reverse the usual order of things by feeding upon insects Plants that feed upon insects are by no means so numerous as insects that consume plants, yet at least five hundred species of entomophagous plants are known (Kerner and Oliver 1895) Charles Darwin was among the first to study these plants, having published an extensive account of them in 1875 This unusual plant-insect relationship is primarily of academic interest, for the number and kind of insect consumed by plants are of little economic significance to man It is of interest chiefly for the intricate and highly specialized anatomical and physiological adaptations possessed by the plants, which enable them to trap the insects and to digest them It illustrates the extent of interdependence between insects and plants and indicates the range of possibility in the evolutionary development of the interrelations between insects and plant pathogens

The mechanisms used by plants in trapping insects are of several different types For convenience, these may be classified into three general groups One group captures insects by means of sticky exudates on the leaf surfaces A second group entraps the insects mechanically by various structural modifications and involves no unusual movement of the plant parts The third group entraps the insects by special movements of modified leaves

The flycatcher (*Drosophyllum spp*) is a good example of the first group The stems of this plant are covered with stalked glands that secrete dewlike drops of a very sticky fluid Insects attracted by this exudate alight upon the stems, become entangled in the sticky fluid, and cannot escape (Fig 7) After an insect is caught, a second type of gland secretes an acid fluid, rich in enzymes, which dissolves and digests the entire insect body with the exception of the chitinous exoskeleton The secreted digestive fluids along with the dissolved insect body, are then reabsorbed by the plant cells The sticky fluid also is temporarily reabsorbed, and the chitinous remains of the insect fall off or are blown away by the wind This plant grows in dry places in Portugal and Morocco, where the natives have long

used it in catching flies, its action being based on the principle
of the well-known "tanglefoot"

The pitcher plants (Sarracenia, Darlingtonia, Nepenthes, etc)
entrap insects by special anatomical adaptations, working on the
principle of a pitfall   The pitfall is formed by elaborate modifi-
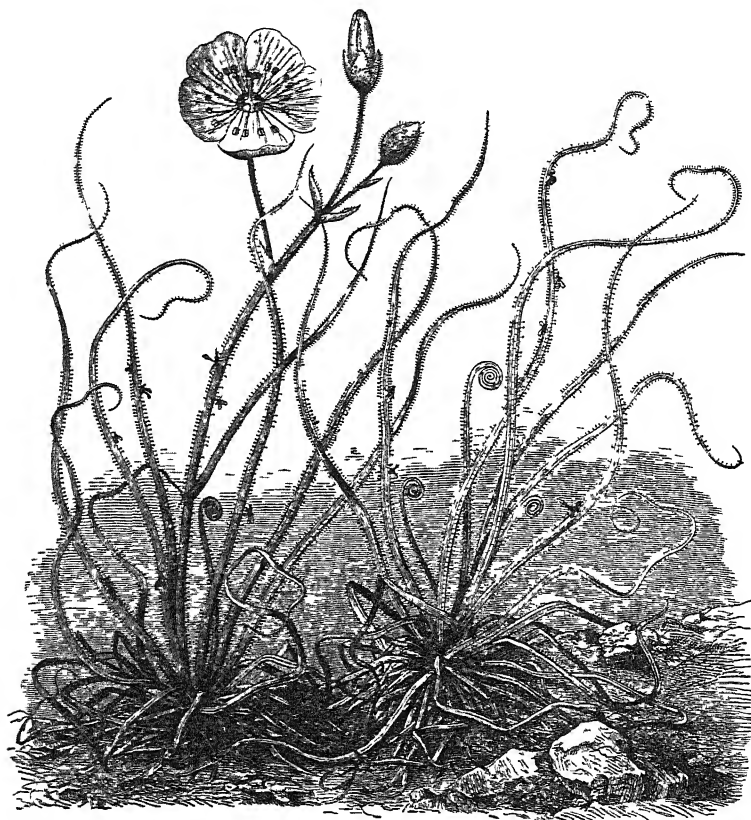
FIG 7 —The flycatcher (Drosophyllum lusitanicum) with insects entangled in the
sticky exudate   (After Kerner and Oliver)

cations of the leaf petioles and assumes a great variety of forms
(Fig 8)   The leaf lamina is usually small and often forms a
canopylike covering over the mouth of the pitfall   The pitfall
consists of three essential parts (1) a device for allurement of
insects, (2) an arrangement for entrapping the insects and for
preventing their escape, and (3) a means of digesting the prey

The allurement is accomplished by means similar to those used by entomophilous plants to attract insects to flowers. Near the opening of the "pitcher," or pitfall, there is often a spot of bright color, usually purple, yellow, green or white. Drops of nectar are secreted around the rim of the pitcher, and there is often a nectar-baited pathway, from the ground to the mouth of the
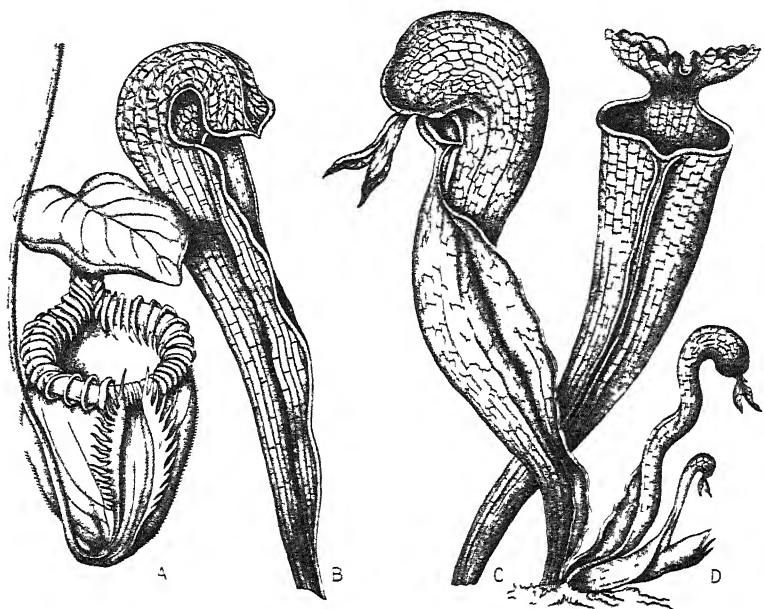
Fig 8—Pitcher plants *A Nepenthes villosa*, *B, Sarracenia variolaris*, *C, Darlingtonia californica*, *D, S lacunata* The petioles are modified to function as pitfalls in which insects are entrapped They are usually partly filled with a liquid rich in proteolytic enzymes that digest the insects (*After Kerner and Oliver*)

pitcher, that attracts wingless insects and leads them to the pitfall

The entrapping device consists of a variety of special structures The inside of the rim of the pitcher is usually formed by a series of smooth bristles pointing downward The inside walls are often lined with similar bristles or with sticky glandular hairs (Fig 9) There is always a quantity of liquid in the bottom of the pitcher into which the insects fall and eventually drown The modified canopylike leaf lamina cuts off the direct light from the opening, adding to the difficulty of escape

The means of digestion have not been determined for all species of pitcher plants   In some species, the presence of pepsin and acid has been demonstrated   Digestive enzymes are probably secreted by most species, but putrefactive bacteria are often found in the liquid, and it is probable that they also are involved in the digestion of trapped insects

The butterworts (*Pinguicula spp*) catch insects in a manner similar to that of *Drosophyllum* except that a definite movement of the leaves is involved   There are about forty species of this plant found mostly in moist locations in arctic and subarctic regions   The plant grows as a rosette with flat oblong leaves
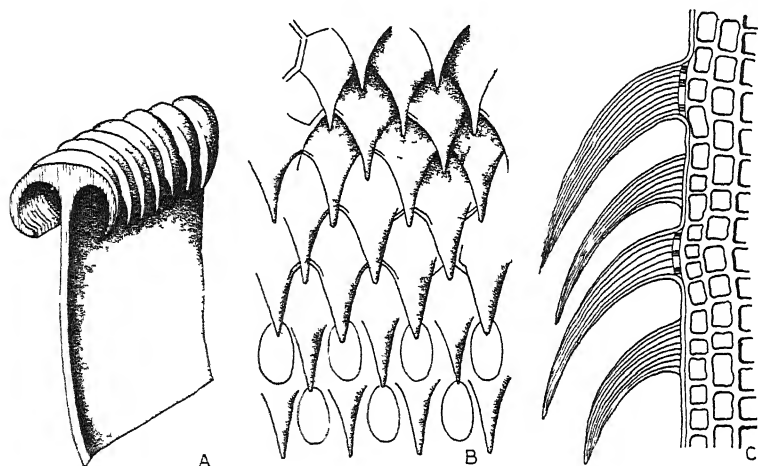
Fig 9 —Downward-pointing spines found along the inner walls of the pitfalls of various species of pitcher plant   (*After Kerner and Oliver*)

lying prostrate on the ground   The upper surface of each leaf is covered with two types of gland, a stalked one secreting a sticky fluid that attracts and holds the insect and a sessile one that secretes the digestive fluid (Fig 10)   The latter fluid is secreted as a direct response to the specific stimulus of a foreign nitrogenous substance present on the leaf   After the insect is caught, the edges of the leaves usually curl upward and inward, covering the smaller insects or pushing the larger ones toward the center of the leaf where the glands are more numerous   The digestive fluid is rich in the enzyme causing rennet coagulation of milk   The plant is said to have been used by the Laplanders as an addition to milk in making a popular milk delicacy

The sundews, comprising the various species of *Drosera*, have a very delicate mechanism for entrapping insects. The insects
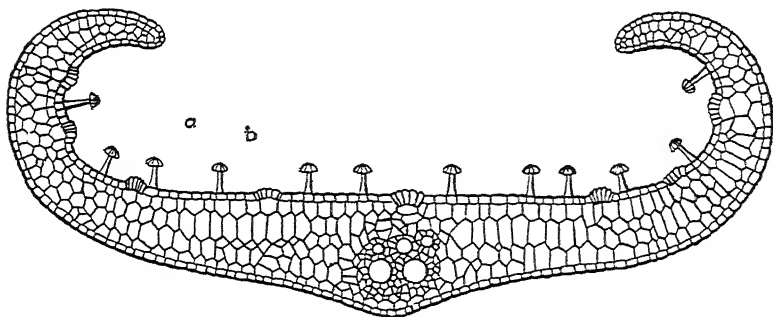
FIG 10 —A diagrammatic cross section of a butterwort leaf showing the stalked glands (*a*) which secrete the sticky fluid that entangles the insect When an insect is entrapped the margins of the leaf curl inward toward the mid-vein, and digestive enzymes are secreted by a second set of glands (*b*) (*After Kerner and Oliver*)

are trapped by leaves that grow as a rosette and remain prostrate on the ground (Fig 11) Each leaf of the rosette is broad and spatulate at the tip The upper surface of the broad part of the leaf is covered with about two hundred red tentaclelike filaments, each with a drop of glistening sticky liquid at the apex (Fig 12a) Insects attracted to the glistening drops alight on the leaf and become entangled in the fluid As soon as the insect is caught the tentacles start bending inward in a way that brings their tips with the sticky liquid in contact with the prey Within a few minutes, all the tentacles are pointing inward and touching the insect (Fig 12b, c, and d)

FIG 11 —A plant of the Sundew (*Drosera sp*) showing the rosette of spatulate leaves that catch and digest insects (*After Brown, by courtesy of Ginn and Company*)

The sticky fluid is secreted in increasing amounts and the insect is soon completely covered This movement takes place only in

response to a nitrogenous substance   The response is extremely
specific, as the tentacles will not respond to such objects as sand,
raindrops or other nonnitrogenous matter, yet $\frac{1}{4000}$ part of a
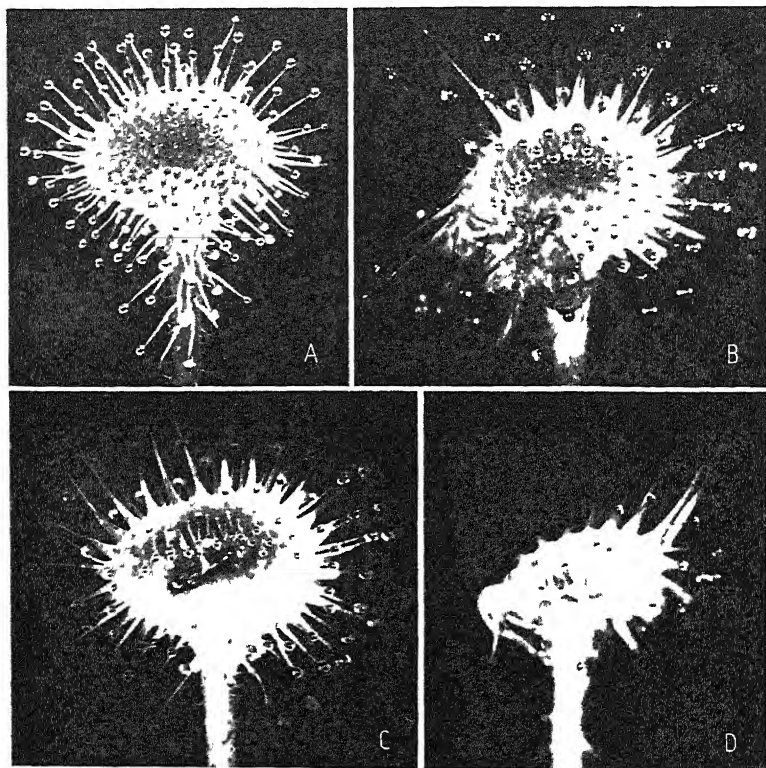
Fig 12 —Leaves of the sundew (Drosera) showing the method of entrapping
insects   *A*, a leaf with the tentacles fully expanded each tentacle bearing a
drop of sticky exudate at the tip, *B* and *C*, leaves showing stages in the capture of
an insect   In *B*, the insect has alighted on leaf and is becoming entangled in
the sticky exudate   Note the tentacles bending inward moving the insect
toward the center   In *C*, the insect has become thoroughly covered with the
exudate and has ceased to struggle   In the final stages, *D*, the tentacles all bend
inward completely enclosing the insect which is digested by enzymes in the
secreted liquid   Approx 3 ×   (*From the instructional sound film, "Plant
Traps, produced by Erpi Classroom Films, Inc*)

milligram of ammonium carbonate will cause them to bend
When the insect victims have been digested, the tentacles straigh-
ten out and resume their original position

   The bladderworts (*Utricularia spp*) catch insects and other
small water animals in a valvular trap   They are mostly rootless

water plants that float near the surface of the water in summer and sink to the bottom as dormant buds in winter. Along both sides of the long lateral stems are borne bladderlike structures open at one end (Fig 13). The open end is surrounded by bristles in position to form a funnel directing the victims toward
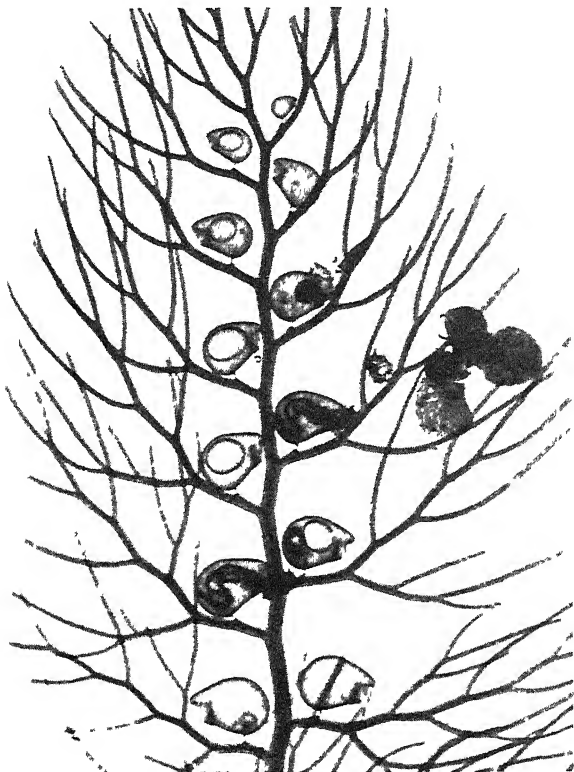
Fig 13 —A portion of a branch of bladderwort (*Utricularia vulgaris*). Five or 10 active bladders contain mosquito larvae. (*After Matheson*)

the entrance. The opening is fitted with a valvelike trap door through which the insects or other organisms are drawn. The mechanism of the trap of *Utricularia* has been studied extensively by several workers, but the investigations of Lloyd (1929, 1932, 1933, and 1935) are the most exhaustive and conclusive. Earlier writers interpreted the trapping mechanism as a simple valvular trap door through which the insects forced their way and then

were unable to escape (Kerner and Oliver 1895), but later work
has shown the mechanism to be of a more complex nature

According to Lloyd, the trap door, when in a set position, rests
upon the outer edge of a threshold and forms a watertight seal
(Fig 14)   The semipermeable walls of the bladder pump the
water out of the lumen, a negative pressure within being thus
formed   This negative pressure is sufficient to cause the walls
to bend inward, and the pressure also holds the door firmly in
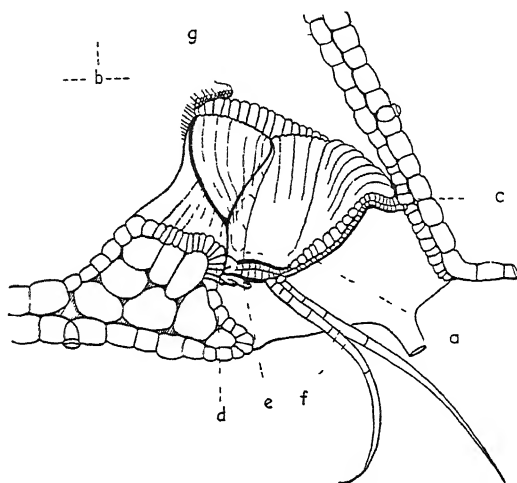
Fig 14 —Diagrammatic sketch of the bladder of *Utricularia* showing the
mechanism of the trap   *a*, door of bladder, *b*, interior of bladder, *c*, attachment
of door to wall of bladder, *d*, threshold, *e*, exfoliated cuticle that makes a water-
tight seal between door and threshold *f*, trigger hairs   When the insect pushes
down on the trigger hairs, they act as a lever, raising the free edge of the door
above the threshold and break the seal   The pressure of the water forces the
door inward and upward against the roof (*g*), and the insect is sucked in with a
stream of water   (*After Lloyd*)

place   The seal of the door is made watertight by a thin veil of
exfoliated cuticle on the threshold against which the door rests
Three or four stiff bristles arise from a thickened plate near the
middle part of the lower free edge of the door and point outward
These bristles are attached at such an angle that a slight move-
ment of their free ends exerts sufficient leverage to raise the lower
edge of the door and break the seal   When this occurs, the
pressure of the water from without forces the door inward, and
the walls of the bladder expand to their normal shape   A
stream of water is drawn into the bladder, and the insect that

moved the trigger hairs is drawn in with it As soon as the bladder is filled with water, the door slowly returns to its original position, and the walls start pumping the water out until the set condition is again reached This usually requires about 15 to 30 minutes The trigger hairs accoiding to Lloyd (1932), are entirely mechanical in their action operating as levers to lift the bottom edge of the door and break the watertight seal The response is not one of irritation as in the Venus's-flytrap
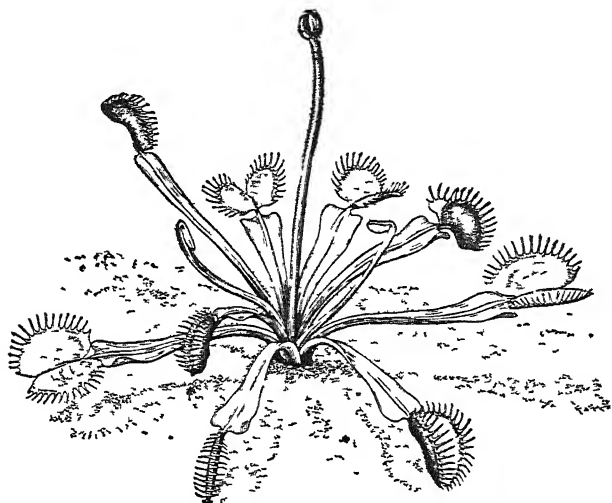
Fig 15 —Venus's-flytrap (*Dionaea muscipula*) Approx $\frac{1}{2}$ × (After Brown by courtesy of Ginn and Company)

The inside walls of the trap are supplied with glands that secrete the usual proteolytic fluid to digest the insects In addition to insects, many other aquatic animals are caught and consumed Mosquito larvae are among the most common insects caught by the bladderworts and it is claimed by some observers (Matheson 1930) that these plants play an important part in mosquito control in certain localities, thus aiding in the control of malaria

The Venus's-flytrap (*Dionaea muscipula*) is perhaps the most striking of all the entomophagous plants This plant occurs in nature only in a narrow strip of country along the east coast of North America in and near peat bogs It like the sundew, grows in the form of a rosette (Fig 15) Each leaf consists of a flat spatulate petiole and a roundish lamina divided by the mid-rib

into two symmetrical halves inclined to each other at an angle
of 60 to 90 degrees, like a half-open book   The margins of the
lamina bear from ten to twenty long sharp spines   In the center
of the upper surface of each half of the leaf, there are three
shorter spines, or trigger hairs   The entire upper surfaces are
covered with still shorter glandular structures that are colored
purple and are capable of secreting a sticky liquid (Fig 16)

When the insect attracted to the leaf by the purple color and
the sticky liquid touches one of the six spines in the center of
the leaves the two lamina fold together tightly and the insect
is entrapped (Fig 16*B*)   The movement is rather slow, 10 to 30
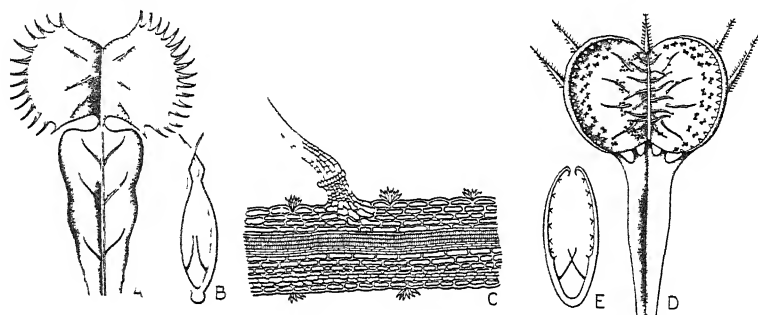
Fig 16 —The entrapping apparatus of Venus s-fly trap and the closely related
A'drolandia   *A*, an expanded leaf of Venus s-fly trap *B*, a cross section of a
closed leaf *C* one of the sensitive bristles of the upper surface of the leaf, *D*,
an expanded leaf of *Aldrolandia* *E*, section of a closed leaf   (*After Kerner and
Oliver*)

seconds being required for the trap to close completely, but the
interlocking spines along the margins prevent the escape of the
insect, and the trap is very effective   As soon as the insect is
trapped, the glands begin secreting the digestive fluids   The
leaf remains closed until the soft tissues of the insect body are
completely digested and the liquid reabsorbed a process that
may require two weeks or more   The leaf then opens and is soon
ready to entrap another insect

These examples of entomophagous plants will suffice to illus-
trate the exceedingly complex and intricate nature of this type
of interrelationship between plants and insects   It is evident
that the entomophagous habit of these plants must have arisen
through a long process of evolution   It is significant that
practically all species of entomophagous plant are found in nature
on soils deficient in available nitrogen   In all probability, the

need of a richer source of nitrogen by the plants has been the directing influence in the origin of the relationship

Nematode-entrapping Fungi—Although nematodes are not insects, they may serve as vectors of pathogenic fungi as pointed out in Chap XI   In view of this fact, it is of interest to know that certain fungi have evolved special adaptations for entrapping and consuming nematodes   Sherbakoff (1933) has described a remarkable soil fungus (*Anulosporium nematogenum*) with ring-shaped spores that function as nematode traps   The ring-shaped conidia that are set free in the soil have a diameter somewhat less than that of a nematode s body   The nematode in moving through the soil gets a ring over the tapering anterior part of its body but is unable to pass entirely through it   By the movement of the nematode the ring is pushed farther and farther back over its tapering body, forming a distinct constriction The conidia then germinate and send hyphae into the nematode s body which is rapidly consumed by the fungus   Further studies of related nematode-entrapping fungi have been made by Drechsler (1933*a, b c*, 1934, 1935 1936), Couch (1937) Lintord and Oliveira (1938) and Lintord and Yap 1939)

3 ENTOMOPHTHOROUS PLANTS

Insects, like other forms of life, are subject to disease   In general, the diseases of insects are caused by the same kinds of microorganism that affect other animals or plants namely, bacteria, fungi, viruses and protozoa   The bacteria and fungi are plants, the nature of the viruses is not definitely known and the protozoa belong to the animal kingdom   Some of the plants that cause diseases of insects affect injurious species and benefit man by aiding him in the control of these pests   Other diseases attack such beneficial insects as the honeybee or the silkworm and are detrimental to the interests of man   The diseases of insects are so numerous that a discussion of them all is not practical here   But with the view of illustrating another insect and plant relationship, a few representatives will be described For more extensive treatments of the subject see Paillot (1933) and Sweetman (1936)

Bacterial Diseases of Insects—The best known bacterial diseases of insects are probably those that affect the honeybee European foul brood is an infectious septicemic disease of honey-

bee larvae and is caused by *Bacillus alvei* Cheshire and Cheyne
Affected larvae become soft and lose their normal shape and
color   At first they turn yellow or gray and eventually dark
brown   The internal tissues are transformed into a viscid liquid
American foul brood of bees is a similar disease caused by *Bacillus
larvae* White   Both diseases are of considerable economic impor-
tance causing much loss to the beekeeper of both Europe and
America (White 1920*a*, *b*)   Diseases of similar nature have been
described in a few instances as affecting injurious insects   *Bacil-
lus sphingidis* White is credited by White (1924*a*) with causing a
disease of this nature on the tobacco hornworm (*Protoparce
sexta* Johan) and the tomato hornworm (*P   quinquemaculata*
Haw)   A septicemia of cutworms caused by *Proteus noctuarum*
(White) Bergey *et al* has been described also by White (1924*b*)

A disease of this general type was discovered on grasshoppers
by D'Herelle (1911, 1912) who described the bacterial pathogen
and named it *Coccobacillus acridiorum*   D'Herelle advocated
the use of the disease in controlling grasshoppers   It was claimed
that the cultures could be made more virulent by successive
passage through grasshoppers inoculated by needle injection
Suspensions of the virulent bacteria were used in spraying
infested fields and the advance ranks of the migratory hoppers
Quick and successful results were claimed by D'Herelle, but
extensive trials made later in many parts of the world have
failed to demonstrate the effectiveness of this method of grass-
hopper control (Kraus 1916)   Barber and Jones (1915), who
were unable to verify the claims of D'Herelle, demonstrated that
the bacteria were virulent when injected into grasshoppers but
that they were not effective when sprayed upon the insects
without wounding

Fungus Diseases of Insects.—A relatively large number of
fungi are known to cause diseases of insects   Only a very few of
them can be discussed here   Fungi pathogenic to insects are
found in the Phycomycetes, Ascomycetes, and Fungi Imperfecti
The Basidiomycetes apparently contain no insect pathogens of
importance   The Phycomycetes include one order, the Ento-
mophthorales, all members of which are exclusively parasitic on
insects   One of the best-known genera of this order of entomoph-
thorous fungi is *Empusa* which contains about forty species,
mostly parasitic on flies   *Empusa muscae* Cohn is the species

affecting the common housefly   The disease appears most fre-
quently in late summer and fall when the weather is cool and
the vitality of the fly is low   At this time the parasitized and
dead flies may be observed adhering to window panes and other
objects surrounded by a halo of white translucent spores that
have been shot off from the fungus growing in the body of the
insect (Fig 17)   The spores are sticky and adhere to any object
they touch, including the bodies of other insects   The spores
germinate, and the mycelium penetrates directly through the
cuticle of the insect and reaches the blood cavity where hyphal
segments are formed   The segments are dispersed in the blood
throughout the body until the entire internal parts are destroyed
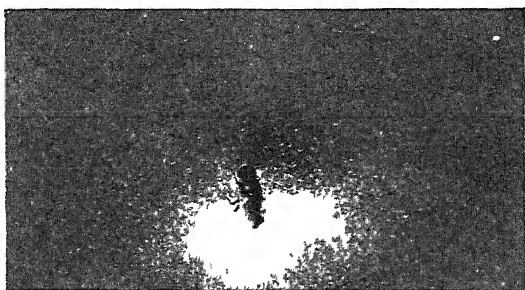
Fig 17 —A fly killed by *Empusa muscae*   The dead fly stuck to a pane of
glass by the fungus, is surrounded by a white zone of spores that have been
shot off   (*From Sweetman, ' Biological Control of Insects,' by permission of the
Comstock Publishing Company*)

The spores are formed on the surface of the insect and forcibly
abjected from the sporophores

  Grasshoppers, aphids and other insects are often parasitized
by species of *Entomophthora*   These fungi usually attack the
insects when the weather is both hot and humid and when the
insects are overcrowded   Under such favorable conditions
the disease may spread rapidly, killing large numbers of insects
and it is probably an important factor in natural control of many
insect species   Periodic attempts have been made to use the fun-
gus in artificial control of grasshoppers   The fungus has been
cultured and sold in tubes for use by spraying on insects in the
field   The attempts have been based on the theory that if an
epizootic is started, the disease will effectively destroy the insects
in sufficient numbers to effect practical control   In practice,
however, the attempts have met with very little success

There is abundant evidence that naturally occurring epizootics of insect diseases serve as important means of natural control, but man has not been very successful in producing artificial epizootics   Claims of success usually have been based on insufficient evidence, and in most cases the method has not withstood careful and critical investigation   In general, it has been found that the fungus is normally present in sufficient quantity to start an outbreak if other conditions (high temperature, high humidity, and overcrowding) are favorable   If these conditions are not favorable, the application of additional inoculum is of little or no avail   Numerous attempts have been made with many different diseases of insects, but this has been the conclusion reached in nearly all careful efforts to evaluate the effectiveness of this method of insect control   The most promising outlook for the use of insect diseases in the control of insects is by introducing the insect pathogens into a locality where they do not normally occur

In certain sections of Florida, several species of fungus are very important in the natural control of the citrus white flies [*Dialeurodes citri* (Riley and How) and *D citrifolii* (Morg)]   The abundant rainfall and high temperatures in summer are very favorable for fungus development, and the summer broods of the insects usually are kept under control (Morrill and Back 1912)   The importance of the fungi in the control of the insects is evident when the citrus trees are sprayed with Bordeaux mixture   The spray controls the fungi, and the white flies increase with abnormal rapidity   The two most important fungi are *Aschersonia aleyrodis* Webber and *A goldiana* Sacc and Ellis   The former known as the "red" Aschersonia, attacks both species of white fly, while the latter, known as the "yellow" Aschersonia, affects only *D citrifolii*   In 1915, the Florida Plant Board began furnishing cultures of these fungi to the growers for use in infesting the orchards to increase the efficiency of control   Infestations may be started in an orchard either by spraying the trees with a suspension of the fungus spores or by pinning leaves with infested insects to the leaves of noninfested trees (Watson and Berger 1932)

One of the more recently reported efforts to control an insect pest by a fungus disease is that of Dustan (1924), dealing with the control of the European apple sucker *Psylla mali* by *Ento-*

mophthora sphaerosperma   The European apple sucker is not a native of North America and was first observed in 1919 in Nova Scotia, where it proved to be destructive in apple orchards   In the following year, local epizootics of the fungus diseases were observed   In orchards where the disease was present, the insects were so reduced in numbers that little injury was caused to the apple trees   In 1922 and in 1923, attempts to hasten the spread of the disease were made by introducing inoculum in the form of diseased insects into orchards where the disease had not been observed   It was stated

Usually about a week after a ' planting" had been made the fungus began to appear in the orchards under experiment   Once started it spread very quickly and within two or three weeks, depending, of course, on the weather conditions was generally distributed throughout the orchards   At this time no disease had appeared in the checks, proving conclusively that the outbreaks in question were due solely to the artificial spread of the fungus

The success in this case led to the recommendation that such "plantings" of diseased material be made by those orchardists who were troubled by the apple sucker   The success obtained by Dustan may possibly be explained by the fact that the insect was a recent importation into North America and that on account of unfavorable weather conditions the spread of the disease had not kept pace with the spread of the insect   If this were true, his "plantings" would have introduced the disease into regions where it had not previously been established   In any event it appears that the disease is an important factor in the natural control of the insect, and if it were not present, the insect would cause much greater damage than it does

Among the Ascomycetes, the genus *Cordyceps* contains about two hundred species, most of which are parasitic upon insects   The fungus mycelium permeates the entire body of the insect and forms aerial hyphae and conidia over the surface   The conidia vary with the species and may be of the *Penicillium*, *Verticillium*, or *Isaria* type   The diseases caused by these fungi are often referred to as the "Muscardine" diseases

The mycelium within the body of the insect is eventually transformed into a sclerotium that keeps the approximate form of the insect   The fungus survives the winter in this stage usually in, or on the surface of the soil, and in the spring a stalk-

like stroma arises from the sclerotium (Fig 18)   The perithecia
are borne embedded in enlargements at the end of the stroma,
from which the ascospores are liberated into the air   A species of
Cordyceps is often found on the white grubs (*Phyllophagus spp*)
and may be a natural control factor in dense populations

The Laboulbemiales of the Ascomycetes include a group of
highly specialized fungi, all obligate parasites on insects   They
are of academic interest only   They are not fatal to the insect

Fig 18 —*Corayceps sp* on larvae of the codling moth showing the stalklike
stromata growing from the dead insect   (*After Metcalf and Flint*)

and apparently cause little or no injury   The fungi do not
penetrate the insect body but are fastened to the integument by
small "holdfasts   and derive their nourishment through minute
holes in the body integument   They form small hairy or velvety
patches on various parts of the insect's body   They are often
highly specialized as to the particular part of the body affected,
some species being confined entirely to one segment or to certain
legs of a single species of insect

The vegetative mycelium is much reduced, and the reproduc-
tion is entirely by ascospores, a highly specialized type of sexual

reproduction similar in many ways to that of the red seaweeds (Florideae) Some species are homothallic, and others are heterothallic

Infection occurs only when one insect comes in close contact with an infected one most commonly during copulation The ascospores, covered with a sticky matrix are forced out of the perithecia and adhere to the insect's body A holdfast is formed and when food relations are established the spore divides and grows into its mature differentiated structure The best and most extensive account of these interesting fungi is that of Thaxter (1896, 1908)

Virus Diseases of Insects —Some of the most virulent diseases of insects are caused by viruses Lepidopterous species being especially subject to them The best known virus diseases of insects are those affecting the silkworm (*Bombyx mori* L) the gypsy moth (*Porthetria dispar* L), and the nun moth (*Lymantria monacha* L) The wilt disease (*grasserie* or *Gilbsucht*) of silkworms, is extremely destructive and is often a limiting factor in silkworm culture The similar wilt diseases of the nun moth and of the gypsy moth also occur in epizootic proportions and constitute important factors in the natural control of these insect pests

Caterpillars affected with wilt become flaccid and the internal organs are completely liquefied The affected tissues are characterized by the presence of numerous very small refractive, crystal-like polyhedral bodies from which the term "polyhedral diseases" has arisen These bodies are protein in nature and may be compound crystals of the infective agent They have been concentrated by centrifuging and washing but have retained their infectious nature The infectious agent in common with other viruses, can be passed readily through certain bacteriological filters

The caterpillars may become infected by ingesting virus-contaminated material or by direct subcutaneous inoculation In nature, the former is the more frequent method of infection, although there is some evidence that the diseases are transmitted by parasitic or predacious insects and mites (Allen 1916) There is some evidence for the conclusion that the virus of *grasserie* may be transmitted through the eggs of the silkworm, although this theory is not accepted by all investigators

Efforts to control noxious insects by the production of epizootics through artificial inoculation with viruses have met with the same doubtful success that has characterized similar efforts with the bacterial and fungus diseases. However, the extent to which other control measures are necessary may be determined by the prevalence of the disease.

Protozoal Diseases of Insects —Although bacteria, fungi, and viruses are the principal causes of insect diseases, there are several well-defined diseases of insects caused by protozoa, the best known of which is probably that affecting the silkworm, caused by *Nosema bombycis* Nag and commonly known as 'pebrine.' The mode of parasitism of the protozoa and the methods by which they are transmitted vary extensively with the different diseases. There is evidence of transmission of some of the protozoal diseases by parasitic or predacious insects. Payne (1933) has reported the transmission of a disease of the Mediterranean flour moth (*Ephestia kuhniella* Zeller) by a Hymenopterous parasite (*Microbracon hebator* Say). The disease is not transmitted by ingestion and is not infectious in the absence of the parasite. Furthermore, the first point of infection is in the ganglion which the parasitic wasp pierces in the act of oviposition. By ovipositing in one larva after another, the wasp becomes especially effective as a vector of the disease.

4 ENTOMOPHILOUS PLANTS

One of the most highly developed and perhaps the most interesting association of plants and insects is that of entomophily or insect pollination of flowering plants. The association has been of great significance in the evolution of plant species and has contributed to the development of many highly specialized relationships between plants and insects. As will be pointed out in some detail in Chap IV, there are many points of similarity between insect pollination and insect transmission of plant diseases and a knowledge of the relationships involved in entomophily is helpful in a study of the problem of insect transmission of plant diseases.

Pollination is the act of transferring the pollen from the anther of a flower to the stigma of the same or another flower and is necessary for fertilization and seed production in practically all seed plants, although there are a few species in which

parthenogenesis occurs   The transfer of pollen from the anthers of a given flower to the stigma of the same flower is termed *self-pollination*   When the transfer is from one flower to another on the same plant it is called *close pollination,* while *cross-pollination* is the transfer of pollen from the flowers of one plant to the stigmas of flowers on another plant   Plants whose flowers can be fertilized by self-pollination or close pollination are said to be *self-fertile*   Some plants are *self-sterile,* a condition in which the flowers can be fertilized only by cross-pollination   It is obvious that when cross-pollination is the rule the probability of hybridization is increased

Some plants have imperfect flowers, one kind of flower (staminate) producing fertile pollen but having no normal ovaries, another kind (pistillate) having normal ovaries but no pollen   These two kinds of imperfect flower may occur on the same plant (monoecious) or on different plants (dioecious)

Cross-pollination stimulates variation by increasing the frequency of hybridization   As variation is a primary factor in evolution, cross-pollination has been a potent factor in the evolution of the flowering plants   Insects as one of the principal agents of pollination, have played an important part in this evolutionary process, and many of the adaptations of flowers to insect pollination are concerned with means of ensuring cross-pollination   In other words, the phenomenon of entomophily has had a great influence on the evolution of flowering plants because, by favoring cross-pollination it has increased the frequency of hybridization and variation   The increased frequency of variation acted upon by natural selection has resulted in the evolution of new adaptations for insect pollination and these, in turn, have further facilitated cross-pollination   Thus, there is a never-ending cycle that has been a very potent factor in evolutionary development of both plant and insect life

Pollination is accomplished in several different ways and plants are sometimes classified on the basis of the principal agent of pollination as follows

1 Hydrophilous—water-pollinated
2 Anemophilous—wind-pollinated
3 Zoidiophilous—animal-pollinated
  a Entomophilous—insect-pollinated
  b Malocophilous—snail- or slug-pollinated

    c Ornithophilous—bird-pollinated
    d Chiropterophilous—bat-pollinated

The anemophilous and entomophilous groups include by far the largest number of species

The Origin of Entomophily—Although there is evidence that some of the primitive angiosperms were insect-pollinated and that certain modern anemophilous species may have arisen from entomophilous forms (Hutchinson 1926), it is generally agreed that the most primitive flowering land plants were wind-pollinated. When pollen grains are disseminated by the wind, pollination is accomplished only when, by chance, a pollen grain falls upon a stigma of a plant of the proper species. Considering the small size of the stigmatic surfaces and the separation of the pollen grains as the distance from the source of supply increases, it is obvious that there is a tremendous waste of pollen. In general, the wind-pollinated species produce very large quantities of pollen. This is true of present-day species, and the abundance of fossilized pollen in the geological records of the Carboniferous age indicates that this was true also of the primitive wind-pollinated plants of that period

Early in the evolutionary development of plants, insects discovered the food value of pollen and began regular visits to the source of supply. Some of the pollen stuck to the bodies of the insects and was transported to other flowers, and thus cross-pollination was accomplished. The pollen was transported by insects directly to the proper stigmatic surface with very little loss of material. The utilization of pollen as food by the insects and the assurance of successful cross-fertilization with a minimum of waste pollen had a survival value to both the insects and the plants. Cross-fertilization stimulated variation, and natural selection fostered and perfected those variations which favored insect pollination. The secretion of nectar, the bright color of flowers, and other characters that attract insects have evolved in this way. These interacting factors have resulted in strong evolutionary forces that have produced the exceedingly complex adaptations existing today between flowers and the insects that pollinate them. It would be out of place here to discuss in detail the thousands of intricate adaptations that evolved as a result of this association, but a few of the most important kinds of variation will be mentioned

Plant Adaptations That Favor Insect Pollination —The bio-
logical and evolutionary significance of cross-pollination has
already been mentioned   Many of the adaptations of flowers
are apparently the result of natural selection and perpetuation
of variations in structure that favored or ensured cross-pollina-
tion   Some of these are independent of insect pollination and

Fig 19 —The transmission of pollinia by a wasp in orchid flowers *(Empactis
latifolia)*   1 the wasp alighting upon a flower 2, the flower as seen from the
front, 3, the same in side view 4 a pair of pollinia with sticky pad at the base,
5, the wasp feeding upon the nectar and pressing its head against the pollinia
6 the wasp leaving the flower with the pollinia adhering to its head 7, the same
insect visiting another flower pressing the pollinia against the stigma, and
effecting pollination   *After Kerner and Oliver)*

apply equally well to wind pollination, but many of them are
also adaptations for insect pollination

In many flowers, the stigma is receptive before its own pollen
is ripe   In such cases, cross-pollination is usually accomplished
before self-pollination is possible   When plants have only
imperfect flowers or physiologically self-sterile flowers, self-
pollination cannot occur, and cross-pollination is obligatory

The pollen of many insect-pollinated plants is sticky or waxy, is not easily scattered by wind, and rarely reaches the stigma in
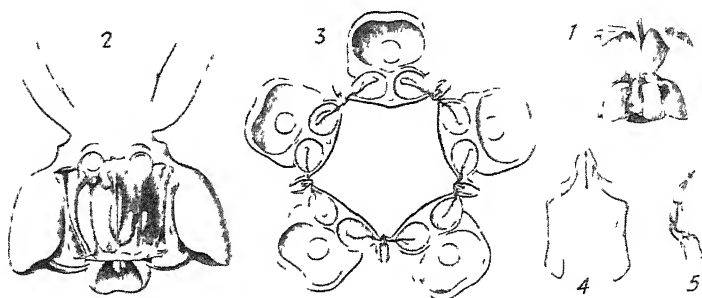
Fig 20 — A flower of the milkweed (*Asclepias cornuti*) showing the pollinia and the mechanism by means of which they become attached to the feet of insects   1, side view of flower, 2, the same magnified and with part of the anther removed to show the pollinia, 3, a cross section of a flower showing arrangement of the pollinia and the clips that become attached to the insects' legs 4, a pair of pollinia and the closed clip mechanism, 5, a pair of pollinia attached to an insect's leg   (*After Kerner and Oliver*)

the same flower, but it is transported readily by insects to other flowers   The specialized pollen masses, or pollinia, found in certain orchids, in milkweeds, and in other plants are structures that ensure cross-pollination by means of special adaptations for translocation by insects   The pollinia are sharply defined masses of sticky pollen specially adapted to insect transportation and borne so that wind dissemination does not occur   These adhere to some particular part of the insect's anatomy and are removed bodily from the stamens   When another flower is visited by the insect in search of nectar, the pollinia are pressed against the stigma, and cross-

Fig 21 —A wasp with pollinia of a milkweed attached to its legs by the clip mechanism shown in the preceding figure   (*After Folsom and Wardle, by permission of P Blakiston's Son & Company*)

pollination is effected   In some cases, the pollinia adhere to the head (Fig 19), in others, they catch on the legs or other parts of the insect (Figs 20 and 21)   However, in all cases, the arrange-

ment prevents the pollen reaching the stigma of the flower in which it is produced but ensures that it will touch the stigma of the flower next visited by the insect

The relative position of the style and stigma in insect-pollinated plants is usually such as to prevent self-pollination As a general rule, the stigmatic surface is borne above the anthers so that the pollen will not drop upon it In some flowers, there are explosive or tripping mechanisms that are set off by the insects in a way which ensures that their bodies become thoroughly dusted with pollen The corollas of the flowers of some species of plants, especially among the orchids, appear to be so modified that pollination is effected by a single species of insect to the exclusion of all others In other cases, several different species of insect may effectively pollinate the flowers of a single species of plant

A further discussion of the innumerable modifications of floral structures concerned with insect pollination and cross-pollination is not possible here The reader is referred to the extensive works of Darwin (1903), Knuth (1909) Kerner and Oliver (1895), Riley (1892), and others

Insect Adaptations That Facilitate Insect Pollination —So far in our discussion of insect pollination we have considered chiefly the modifications of floral structures Similar adaptations exist also among the insects Where there is mutual adaptation, it is not always possible to determine how much of the adaptation is the result of variation in the plants and how much is the result of insect variation Because of the hybridization that occurs so frequently in plants as a result of cross-pollination, it seems reasonable to assume that the plants have been the more variable However, hybridization and variation do occur in insects and natural selection would operate whenever there are variations with a survival value The most striking adaptation of insects for pollination are the specialized bristles that occur in a wide variety of forms and serve for collecting pollen (Fig 22) These bristles are usually localized on that part of the insect's body which is most likely to come into contact with the stigma of the flowers that it usually pollinates The suctorial mouth parts or insects that regularly feed on nectar present well-known adaptations Some insects such as the Pronuba moth (*Pronuba spp*) and the fig wasp (*Blastophaga psenes* L) breed in the ovaries of

the plants that they pollinate   Associations of this kind usually
result in a high degree of interdependence of the plants and their
respective insects and involve highly adapted instincts

The yucca plant is entirely dependent upon the moths for
pollination   Its pollen is produced in sticky masses that preclude
the possibility of wind dispersal   However, pollination is effec-
tively accomplished by the pronuba moths whose breeding habits
reveal striking adaptations of instinct   The female moth
deposits her eggs in the ovary of the flower, and the young larvae
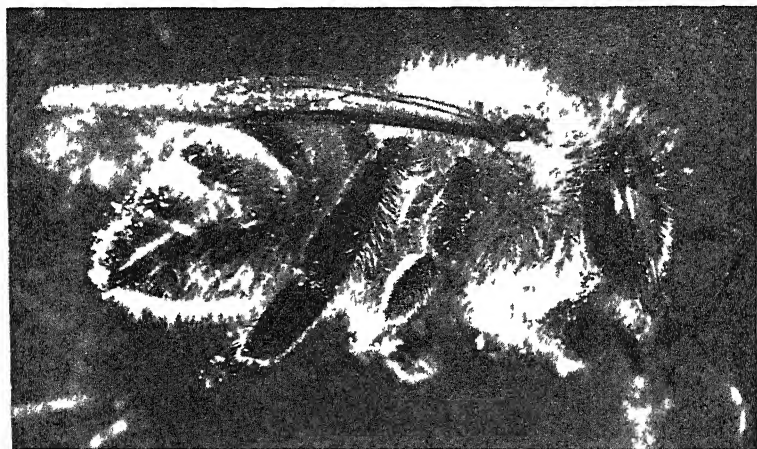
Fig 22 —A honey bee, showing the many bristlelike setae with pollen grains
adhering to them   One of the most important functions of the setae is the
collection and transportation of pollen from flower to flower in which process
the flowers are cross-pollinated   Fungus spores and bacteria adhere to the
setae as readily as do pollen grains   (*Cf* Fig 220)

are dependent upon the fertilized seeds for food   If the flowers
were not pollinated, the seed would not develop, and the larvae
would starve   With unerring instinct, the female moth collects
pollen from one flower before ovipositing into the ovary of a
second one   When oviposition is accomplished, she then stuffs
the pollen into the funnel-shaped stigmatic opening (Fig 23)
Thus the insect not only makes fertilization and cross-pollination
possible, but she also ensures a food supply for the young larvae
Although the larvae feed upon the developing seeds, they do not
consume them all, a supply of seeds sufficient to maintain the
species developing without injury   Without the aid of the moth
no seed would develop

An equally complicated adaptation is found in the relationship between the fig wasp and the Smyrna fig   The so-called "fig flower ' is in reality a whole collection of flowers or an inflores-
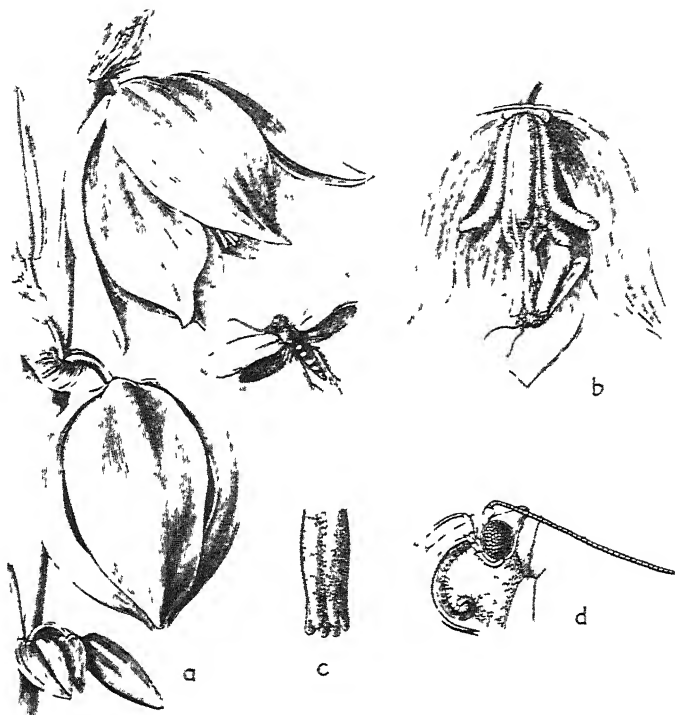
F IG 23 —Insect pollination of yucca by the Pronuba moth   *a* a sketch showing a Pronuba moth *Pronuba yuccasella* and three yucca flowers in various stages of development *b* a yucca flower with three petals removed to show style and stamens   (The moth has oviposited in the ovary of the flower and is stuffing a mass of pollen previously collected from another flower into the funnel-shaped stigmatic surface   *c* an enlarged view of the stigma, *d*, an enlarged view of the head of the female moth showing the mass of pollen grains held by the coiled maxillary palp that is specially adapted for this function (*After Kerner and Oliver*)

cence enclosed within a pear-shaped receptacle a *synconium* (Fig 24)   The female of the fig wasp *B psenes* L) enters the synconium through the eye and oviposits in the ovules of the young flowers   The eggs hatch and the larvae develop in the ovary, which enlarges abnormally, forming the so-called ' galls "

Following pupation the males emerge first and fertilize the females while they are still in the gall   The male dies without leaving the synconium, but the female emerges through the eye and in so doing becomes dusted with pollen   She then enters another fruit, and while in the act of oviposition she pollinates the pistillate flowers   In the edible fig, the styles of the pistillate flowers are so long that oviposition is not successful, and no wasps
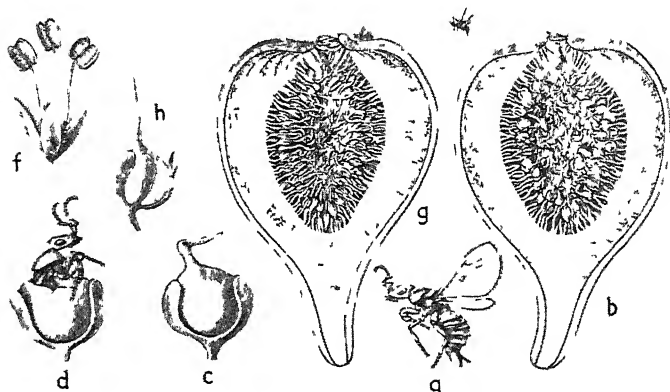
Fig 24 —The pollination of the fig by the fig wasp (*Blastophaga psenes*) *a*, a fig wasp, *b*, a synconium of the caprifig showing the enlarged ovaries of the gall flowers in which the wasps develop, *c*, an enlarged view of the gall flowers of the caprifig showing the short style through which the eggs are inserted by the female fig wasp, *d*, a wasp emerging from a gall flower, *e*, a freshly emerged wasp which has become dusted with pollen from the male flowers (*f*) borne near the "eye" of the caprifig, *g*, a synconium of the edible fig the flowers of which will be pollinated by the wasp about to enter the eye, *h*, the female flower of the edible fig showing the long style which prevents successful oviposition   The insect thus pollinates the fruit of the edible species but is not able to breed in it   They breed in the caprifig which has the short styled flowers   (*After Kerner and Oliver*)

develop in it   Pollination, however, is successful, and the fruits develop normally   The insects breed successfully in the inedible caprifigs, a supply of which is necessary in the cultivation of the edible varieties

It is evident that in this relationship there is a high degree of interdependence between the fig plant and the fig wasp   Neither one can survive without the other   As will be described in Chap VII, this insect is also an important vector of certain destructive diseases of the fig fruit

5 INSECTS AND PLANTS THAT LIVE IN SYMBIOSIS

In the course of the long period of time that plants and insects have shared the available food and space on the earth's surface, many adjustments have been made In numerous cases certain species of plants and insects have become so thoroughly adapted to living together in close spatial relationship that the association has become relatively constant This type of association is usually known as *symbiosis*

We are interested here primarily in those microscopic plants (bacteria and fungi) which are known to live in symbiosis with insects The existence of symbiosis between certain insects and microorganisms has been known for a long time, but the work of Paul Buchner and his students summarized in his book "Tier und Pflanze in Symbiose ' published in 1930 has shown us the astounding universality of the phenomenon and the high degree of development it has reached Buchner's investigations are of great significance to the student of insects in their relation to plant diseases They have shown that symbiosis with microorganisms is to be found in nearly all orders of insects and that in some groups, such as those feeding on plant sap and on wood, it is almost universal In several cases the symbiotic microorganisms are pathogenic to plants Buchner's studies of the subject have yielded sufficient evidence to justify the conclusion that the interrelationships of insects and symbiotic microorganisms are as complex as and of evolutionary significance equal to those between insects and flowering plants The almost universal occurrence of symbiosis between insects and microorganisms in general, coupled with the numerous striking cases involving plant pathogens, makes it imperative that we recognize the importance and significance of the phenomenon in the study of plant diseases The subject is discussed in more detail in Chap III

6 INSECTS THAT DISSEMINATE PLANT PATHOGENS OR AID IN THE DEVELOPMENT OF PLANT DISEASES

This relationship is presented in Chap IV

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CHAPTER III

SYMBIOSIS BETWEEN INSECTS AND MICROORGANISMS AND ITS SIGNIFICANCE IN PLANT PATHOLOGY

Symbiosis is a subject of wide biological interest. The phenomenon is found in some form in almost all classes of plant and animal life and sometimes is essential to the survival of the species. Symbiosis is especially prevalent between insects and microorganisms, where the relationship often reaches a very high degree of development. It has been shown that a number of plant pathogenic microorganisms live symbiotically with their insect vectors, the relationship usually working to the mutual advantage of the associated species. Diseases caused by pathogens that live in symbiosis with insects are sometimes very complex in their ecological relationships. A satisfactory knowledge of the epiphytology of diseases of this kind is rarely possible without a thorough understanding of the symbiotic relationships of the pathogen and its insect vector. Therefore, symbiosis is obviously a subject that cannot be neglected in any comprehensive study of insect transmission of plant diseases.

Symbiosis, a term first used by De Bary (1879), is a broad one and includes all associations in which dissimilar organisms live together in close spatial relationship. It does not imply benefit or detriment to either party of the association. *Parasitism,* in which one organism derives benefit at the expense of the other, is a form of symbiosis usually termed *antagonistic symbiosis.* If the association is mutually beneficial to the associated organisms, it is designated *mutualistic symbiosis* or *mutualism.* When there is little or no direct influence of one organism upon the other, the relationship is called *commensalism.*

It is not always possible to know accurately and completely how much and what kind of influence the organisms have upon one another. For this reason, it is often difficult to use these terms with accuracy. In much of the recent literature dealing with symbiosis between insects and microorganisms, the term

symbiosis has been used in a restricted sense to exclude parasitism and commensalism. Used in this sense, it has essentially the same meaning as mutualistic symbiosis. Nuttal (1923) defines symbiosis as "a condition of conjoint life that is more or less beneficial to the associated organisms or symbiotes" and Shull (1920) defines it as "the association of two species for their mutual benefit." Although there may be some question of the justification for restricting the term in this way the restricted concept has become so well established that it may be very difficult to change it. However, in this discussion the use of the term in the restricted sense will be avoided as much as possible.

The term "symbionts" has been used very generally to designate organisms that live in a state of symbiosis, although some writers prefer to use "symbiotes," maintaining that it is the correct term (Meyer 1925). Symbiote seems to be the better word from the standpoint of etymology, and for this reason it will be used here. Some authors in writing of symbiosis between insects and microorganisms have used symbiont or symbiote to designate the microscopic member of the association, referring to the insect as the 'host.' Unfortunately, the latter term is used with different connotations in both entomology and plant pathology. In order to avoid confusion, the term microsymbiote' will be used in this discussion in referring to the symbiotic microorganism. A good discussion of the origin, meaning, and usage of the above terms has been presented by Hertig Taliaferro, and Schwartz (1937).

Perhaps the earliest recognized and best known example of symbiosis is that between the two microscopic plants found in lichens. The symbiotic relationship between the fungi and algae that make up the vegetative body of the lichens was first extensively studied by De Bary in 1879 and since then it has been the subject of numerous investigations which have shown that the benefits derived by the algae and fungi vary in different lichens. In some species, there is a mutual benefit, in other species the fungi are apparently parasitic on the algae, and instances have been reported wherein the algae are parasitic on the fungi.

Another well-known example of symbiosis between plants is that found in the root nodules on leguminous plants. The bacterial symbiote lives within the tissues of the root on which it causes the globular nodules characteristic of most leguminous

plants   Since the bacteria are able to fix atmospheric nitrogen
a source of nitrogen is provided for the legumes, which in turn
furnish the bacteria with carbohydrates and other materials
necessary for their growth

It is well known also that the roots of most trees and many
other perennial plants are invaded by symbiotic fungi   The
fungus mycelium and the root tissues form specialized structures
known as "mycorrhizae"   These are either ectotrophic or
endotrophic   In the former, the fungi are mostly on the surface
of the root, surrounding it like a sleeve, those of the endotrophic
mycorrhizae occur within the tissues, growing between the cortex
cells   The physiological relationship between the fungi and the
roots has been the subject of much study   The entire subject
has been reviewed extensively by Rayner (1927) and by Hatch
(1937)   The latter concludes that the trees are dependent upon
the fungi for the absorption of nutrients from infertile soils and
that the fungi derive growth-promoting substances and in some
cases simple carbohydrates from the trees

Many lower forms of animal life characterized by a green or
yellowish-green color have been known for a long time   It is now
recognized that the color often is derived from symbiotic green
algae living within the animal tissues   This condition is found
in many Protozoa, Porifera, Coelenterata, Ctenophora, Platy-
helminthes, Annelida, and Mollusca   The fresh-water forms are
associated with green algae and are known as *Zoochlorella*   Those
living in salt water harbor the yellow algae and are called
Zooxanthella

Symbiosis with microorganisms is very extensive among
insects   Buchner (1930) has published an extensive review of the
subject and has described a whole series of symbiotic associations
of widely varying degrees of complexity   He is led to believe
from his studies that this series of symbiotic relationships repre-
sents an evolutionary development, from a simple primitive type
to the more complex associations, which parallels the evolution of
the insects themselves   Thus in the Blattidae, where symbiosis
is universal and of a similar nature in all species, it is believed that
symbiosis arose in the most primitive ancestral forms and has
been transmitted to the more recently evolved forms   In con-
trast to these, the Homoptera possess a variety of types of
symbiosis in different species, a fact indicating that symbiotic rela-

tionships were established relatively late in this order and independently in the different groups within the order

Buchner classifies the various types of symbiotic associations into two main groups (1) *ectosymbiosis*, in which the symbiotic microorganism is found chiefly on the outside of the insect s body, and (2) *endosymbiosis*, in which the microorganisms are harbored within the body of the insect Endosymbiosis is further divided into a progressive series of increasingly complex types on the basis of the localization of the microsymbiote within the insect body These subclasses are as follows

a The microsymbiote develops free in the lumen of the intestinal tract or in intestinal caeca

b The microsymbiote develops within the epithelial cells of the intestinal tract

c The microsymbiote develops in the region of the mesoderm but retains its connection with the epithelium

d The microsymbiote develops within special cells mycetocytes or special tissues (mycetomes without any connection with the intestinal tract

Ectosymbiosis is considered the most primitive type followed by the simpler type of endosymbiosis in which the microsymbiote is found in the lumen of the intestine or in intestinal caeca From this simple type of endosymbiosis, more complex types of endocellular symbiosis have evolved It is believed that the microorganisms entered the epithelial cells, finally invaded the mesoderm, and in the most highly developed types, became localized in mycetocytes or mycetomes, having lost all connection with the intestinal organs A better appreciation of this classification may be had from the consideration of representative examples

Ectosymbiosis —Perhaps the most widely known example of ectosymbiosis is that between the ambrosia beetles and the ambrosia fungi The ambrosia beetles are timber-boring Scolytidae that breed in the sapwood of dying trees The galleries are of various types but the walls are always stained a dark color by the growth of a characteristic fungus that is universally present The fungus is introduced by the beetles into the newly formed gallery where it grows to the exclusion of other fungi The ambrosia fungus fruits by forming masses of glistening white spores on the walls of the larval chambers The developing larvae feed upon the fungus spores, deriving most of

their food from this source   When the new brood of beetles emerges, each beetle carries with it spores of the fungus to be used in starting a new culture in the galleries established in suitable trees   The somewhat similar association of bark beetles and fungi as illustrated in the Dutch elm disease and in the blue stain of conifers (see Chap VII) is another example of ectosymbiosis

The fungus-cultivating ants and termites and their fungus gardens are also examples of ectosymbiosis   Both these groups of insects cultivate fungi in their domatia on specially prepared beds of plant tissue   The growing fungus is utilized as food by the developing young, and when a new colony is established, enough of the fungus is carried along to start a new culture

Endosymbiosis —*a*   The simplest type of endosymbiosis is that in which the microsymbiote develops in the lumen of the intestinal tract of the insect without penetrating the epithelial cells   Excellent examples of this relationship are found among the Diptera, many species of which harbor bacteria that aid the insects in the digestion of the tissues on which they feed   Within this group is found a series of associations of increasing complexity, varying from the relatively simple type between bacteria and the housefly (*Musca domestica* L), the blowfly (*Calliophora vomitoria* L), and the seed-corn maggot (*Hylemyia cilicrura* Rond) in which there are no special caeca for harboring the microsymbiote, to the more complicated type between the olive fly (*Dacus oleae* Rossi) and its microsymbiote in which highly specialized caeca, or "fermentation chambers," are provided for harboring the bacteria and ensuring contamination of the eggs (see Chap VI)

b   A good example of a microsymbiote localized in the epithelial cells of the insect is afforded by the yeast associated with the flour beetle (*Sitodrepa panicea* L)   Certain cells (mycetocytes) along the walls of the intestinal caeca of this insect are filled with actively growing yeast cells   The yeasts, which aid the beetles in digesting starchy food materials, are also found in the intestinal lumen and in special caeca from which the eggs are surface-contaminated when deposited

c   In the weevils, represented by *Hylobium abietis* L , the microsymbiotes are found within groups of cells (mycetomes) adhering closely to the walls of the intestinal tract but having no direct

connection with the lumen   These are often so situated that
they resemble the caeca, or fermentation chambers, that harbor
the microsymbiotes in the more primitive forms described above
This resemblance has suggested that they may have originated as
a modification of the fermentation chambers, the walls of which
have been transformed into mycetomes   Although the function
of these mycetomes is not conclusively known, they are sup-
posed to be concerned in digestion of the wood consumed by the
weevils

d The most highly developed type in this series is represented
by those insects which harbor microsymbiotes in specialized
groups of cells, or mycetomes located deep in the body cavity
and having no connection with the intestines   This situation
is especially prevalent in those sucking insects which commonly
feed on the sap of plants such as aphids, scale insects, and leaf
hoppers   The so-called   pseudovitellus" of the aphids is the
classic example of a mycetome of this type   This organ, consist-
ing of a mass of large fatlike cells found in the abdomen of aphids
was described by Huxley in 1858, but it was not until 1910 that
its true nature was discovered independently by Peiantoni and
Sulc   In this association the microsymbiotes serve the insect by
absorbing waste products, such as urates, and the insects provide
the microsymbiotes with food and protection

When insects and microorganisms live in symbiosis, some pro-
vision is necessary to ensure constant association of both sym-
biotes   Obviously the greatest necessity is to ensure the
transmission of the microsymbiote from one to the next genera-
tion of the insect   This is accomplished in a variety of ways
Where the symbiotic microorganism is cultivated outside the
body, the insects always carry the microsymbiote with them when
establishing a new colony   In many cases, the transportation
appears to be a matter of chance the microorganisms adhering to
the surface of the insect's body or being carried in the contents
of the intestinal tract and being passed out with the excreta in a
viable condition   This is the method used by the bark beetles
and many of the ambrosia beetles   The females of some tropical
ambrosia beetles are said to carry spores and mycelium of the
ambrosia fungus between special brushlike structures on the front
part of the head (Strohmeyer 1911)   In the case of the fungus-
cultivating ants, the female stores in her infrabuccal pouch a

mass of the fungus which is used as "spawn" in starting a new
fungus garden

More highly specialized devices for transmission of the micro-
symbiote are found in insects with endosymbiosis   Here there
appears to be a series of increasingly complex arrangements
The simplest arrangement is that found in certain dipterous
insects in which the reinfection of larvae is left entirely to chance,
the eggs usually being deposited in places where the microorgan-
isms are abundant   In certain other insects, the anal and the
genital openings are so close together that the eggs become
surface-contaminated from the excreta at the time of oviposition,
no special organs for ensuring contamination being necessary
Next in order of complexity are those in which there are anatom-
ical modifications of the female body involving special organs that
function to ensure contamination of the egg   These organs differ
considerably in different species, but all involve the accumulation
of the microsymbiote in some sort of diverticulum located near
the genital opening in a way that ensures the contamination of
the eggs at the time of oviposition   In some species, contamina-
tion depends upon the normal pressure of the egg as it passes
through the oviduct   In others, the diverticulum is equipped
with special muscles that force the microorganism out onto the
egg surface   Some of these diverticula arise from the anal pas-
sage, some are intersegmental in origin, and in certain species the
bursa copulatrix is used for this purpose

In the majority of cases, the young larva comes in contact with
the microsymbiote only after the egg has hatched and the larva
has had an opportunity to ingest the microorganism from the
shell surface   But in some insects, as in *Dacus oleae*, the bacteria
penetrate the egg through the micropyle, and the larva is inter-
nally contaminated before the egg hatches

In those insects in which the intracellular symbiotes are located
in mycetocytes or mycetomes contained in the body cavity, the
eggs generally become infected internally before oviposition, the
microsymbiote entering the immature eggs through the nurse
cells   Some of the scale insects offer good examples of this kind
of transmission   Mansour (1934a) has described a different
process found in three beetles (*Rhizopertha dominica* F , *Sinoxylon
ceratoniae* L , and *Bostrychoplites* Marsh) in which the micro-
symbiotes invade the testis lobes, multiply and mix with the

sperms, and during copulation pass into the *bursa copulatrix* of the female. From here they penetrate through the micropyles of the fully formed eggs during oviposition.

In some of the parthenogenetic insects reproducing vivipariously, the young embryo is infected before birth. This is the rule among the aphids. In the Pupipara and in certain other Diptera (Glossina) that reproduce viviparously, the young larvae are contaminated through the so-called "milk glands" which nourish them before birth.

THE NATURE OF THE SYMBIOSIS BETWEEN INSECTS AND MICROORGANISMS

Most, if not all the symbiotic associations between insects and microorganisms rest upon a physiologic basis and probably should be classed as mutualistic symbiosis. The associations however are very complex, and in only a very few cases is there enough known about the physiology of the symbiotes to justify a final conclusion. In reality it is practically impossible to draw a sharp line between parasitism and mutualism in most instances of symbiosis of insects with microorganisms. Well-defined cases of insects being parasitized by microorganisms are known, and there are equally well-defined examples of mutualistic symbiosis, but between these two there is a whole series of intergrading types that permits no sharp separation. Perfect mutualistic symbiosis might be considered as an association in which both symbiotes are so completely adapted to a common life that neither one can survive in the absence of the other. This condition has been called *obligate symbiosis*. Such relationships are extremely rare. There are, however numerous associations in which both symbiotes are constantly associated in nature and in which the survival of one of the symbiotes is dependent upon the presence of the other. In these cases it usually can be demonstrated experimentally that the other symbiote may survive alone under proper conditions, although it may never be found alone in nature. Beginning with these highly specialized associations we find all degrees of interdependence down to very casual associations that are by no means fixed or constant.

Many students of symbiosis have concluded that mutualistic symbiosis arose through an intermediate stage of parasitism

on the part of one of the associated organisms According to
this theory, the parasitized member acquired an increasing
degree of immunity which, after a period of time, resulted in
mutual adaptation to a common life If this theory is correct,
the microsymbiotes were originally parasitic on the insects, the
latter having acquired immunity sufficient to establish a fairly
constant equilibrium

Buchner (1930) expresses the opinion that, in all cases of
symbiosis between insects and microorganisms, it is the insect
which dominates the situation The microsymbiote is provided
with food and shelter but in all other respects is dominated by
the insect that derives the greater benefit Buchner, therefore,
speaks of the association as a "master-servant" relationship

The frequency with which symbiosis occurs in nature has
led some biologists to suggest that the phenomenon has a general
and fundamental significance in all forms of life As a matter
of interest the hypothesis formulated by Portier (1918) should
be mentioned, although it has been generally discredited
Portier held all higher forms of life to be the results of symbiosis
He recognized two main groups of living organisms, separated
on the basis of the occurrence of intracellular symbiosis the
autotrophic forms which included only the simplest unicellular
organisms such as bacteria, and the *heterotrophic* forms which
included all higher plants and animals, the tissues of which,
according to Portier, constantly and universally contained intra-
cellular symbiotic microorganisms Some of these symbiotes,
he claimed, could be isolated and grown in artificial culture while
others had become so thoroughly adapted that they could not be
isolated and cultured He interpreted the latter as identical
with the mitochondria or other plastids These intracellular
symbiotes according to Portier, play a very important role in all
biologic processes such as sexual fertilization and disease resist-
ance and even in the origin of species The theory was given
some support by the Italian biologist Pierantoni and has been
elaborated by Wallin (1927) in his book "Symbionticism and the
Origin of Species "

In the consideration of mutualistic symbiosis, one is interested
in knowing the physiological interrelationships and the relative
amount of benefit derived by each party of the association
However, so little is known of the physiology of either the

insects or the symbiotic microorganisms that not much accurate information is available Uvarov (1928) has summarized the literature on the nutrition and metabolism of insects up through 1927, emphasizing the great lack of accurate and specific information on the subject For our purposes it will be necessary to discuss only a few of the facts and theories that have come from some of the more important investigations

Apparently the benefits derived by the insects from the association are largely a matter of nutrition Several investigations have shown that symbiotic microorganisms aid insects in the digestion of their food The microsymbiotes apparently produce enzymes, vitamins or other substances that the insects themselves cannot produce One of the more clear-cut cases of this type is that of the wood-eating termites and protozoa investigated by Cleveland (1923 to 1934) who demonstrated that, for the digestion of cellulose these termites are dependent upon protozoa found in an enlargement of the hind intestine When the termites were defaunated and reared in the absence of the protozoa they were unable to digest cellulose

In support of the theory that the microsymbiotes are largely concerned with nutrition Buchner (1930) points out that the insects which most universally harbor microsymbiotes can be grouped into the following four general categories on the basis of the type of food utilized

1 Those that utilize food rich in carbohydrates (especially cellulose) and poor in nitrogen
2 Those that suck the sap of plants
3 Those that feed on blood of vertebrates
4 Those that feed on horny substances hair feathers etc

Baumberger (1919) made extensive experiments with Drosophila and concluded that symbiotic yeasts were necessary for the normal development of the larvae He concluded that the larvae utilized the yeast as food and that the chief role of the yeast was in the synthesis of some necessary food substance or the concentration of available nitrogen He held that the nitrogen content of the plant tissues was not sufficient to allow the completion of the life cycle in the normal length of time He showed that the edible portion of banana tissue contained about 1 3 per cent protein while the yeast cells contained about 11 per

cent   These general conclusions conform with those reached by
Loeb and Northrup (1916) and Northrup (1917)

Leach (1926, 1931) and Huff (1928) have shown that the
bacteria associated with the seed-corn maggot, the vector of
potato blackleg and other soft rots, aid the insect in the digestion
of the plant tissues on which it feeds   Sterile maggots reared
from surface-sterilized eggs do not develop normally when fed
on sterile plant tissue such as a potato plug or steamed bean
seeds, but if the bacteria are present they grow well and pupate
normally   They will grow and pupate also on tissues previously
decayed by the bacteria and later sterilized by heat or on sterile
germinating beans or pea sprouts in which the stored foods are
being translocated into the growing shoots   These facts indicate
that the chief function of the bacteria is to digest the plant tissues
and make them available as food for the larvae

It has been shown by numerous investigators that many
insects feeding on decayed wood derive their nourishment
primarily from the fungi found in the wood   The nitrogen
content of the wood appears to be the limiting factor in the
nourishment of many wood-eating insects   Since fungi have a
higher nitrogen content than wood, those insects feeding on
decayed wood are able to complete their life cycle in a shorter
period of time than those feeding on sound wood

Buchner (1928) maintains that the intracellular symbiotes of
wood-eating beetles digest cellulose that the insects alone could
not digest   This interpretation is questioned, however, by
Mansour (1934*b*) and Mansour and Mansour-Bek (1934) who
claim that the relationship is not one of mutualistic symbiosis
but is to be interpreted as commensalism   Muller (1934)
interprets the relationship as a very weak regular hereditary
parasitism

Uvarov (1928) and Koch (1933) conclude that the micro-
symbiotes in many instances are utilized as food by the insects
and serve as a source of vitamins that the insects require but
cannot synthesize   Bacot and Harden (1922) investigated the
role of yeast in the nutrition of Drosophila and concluded that
the insect requires vitamin B for complete development and that
the vitamin is normally obtained from the yeast   These con-
clusions have been confirmed by Van't Hoog (1935), who was
able to grow the insects successfully in synthetic medium,

concluding that in nature the yeasts commonly supply one or more of the B vitamins and some undetermined substance in the unsaponifiable fraction of fats

It has been suggested that those microsymbiotes which are associated with the Malpighian tubules play a part in decomposing and disposing of the waste products of the insect's metabolism Some suggest without supporting evidence, that the microsymbiotes fix atmospheric nitrogen for certain insects that feed on materials low in nitrogen content (Cleveland 1925*a*) Others believe that the microsymbiotes found in mycetomes of the Homoptera are concerned in making available the food materials stored in these structures for the nourishment of the developing ova It is even suggested that they may be concerned in the initiation of embryonic development in those insects that reproduce parthenogenetically

The fungi associated with the bark beetles develop extensively in the bark surrounding the brood galleries and modify greatly the microenvironment by increasing the moisture content of the inner bark and causing the outer bark to separate from the wood Leach, Orr, and Christensen (1934) considered this ecological influence of decided value to the insect Person (1931) has presented evidence to show that the yeasts associated with the bark beetles ferment the sap of infested trees and produce a distinct odor that attracts other beetles making it possible for the insects to attack the trees gregariously This obviously would be of definite value to the insects because individual insects are rarely able to establish themselves in normal, vigorous trees

In spite of the scarcity of experimental evidence there are several obvious ways in which the microsymbiote profits by the association In the first place the microorganisms are assured a constant food supply and effective protection against such unfavorable environmental factors as excessive heat, light, and desiccation If the microorganisms is not an obligate symbiote, it frequently is associated with the same food substance utilized by the insect Organisms of this kind usually depend upon the insect for dissemination and transportation to the source of food Also, if the microsymbiote happens to be a plant pathogen it may be dependent upon the insect for ingress into the plant tissues (*cf* the Dutch elm disease bacterial wilt of cucurbits, potato blackleg etc)

There is obviously much variation in the functions of the different symbiotes and the benefits derived by each, yet the evidence seems to indicate more than a fortuitous relationship It would be difficult to conceive of such complicated and specialized associations as arising through chance and having no biological value   The associations are certainly the result of a gradual evolutionary development and have persisted because of some survival value, although the survival value may have been based on any one of many different functions   There is no reason to expect that the functions and benefits should be the same in all cases

Symbiosis gives rise not only to physiological adaptations but to structural modifications as well   There have been numerous anatomical adaptations on the part of the insect for harboring and transporting the microsymbiote and for ensuring its transmission from generation to generation   Among these are the various intestinal caeca, mycetocytes, and mycetomes, examples of which have already been described

The structural modifications on the part of the microorganisms are not so evident   The fungi cultivated by the leaf-cutting ants develop peculiar club-shaped hyphal tips that are eaten by the ants   These structures are called *bromatia* (Fig 34) and are said by Wheeler (1923) and others to be the result of some special form of cultivation by the ants   As a rule, the intracellular microsymbiotes are very simple in structure and show no special morphological adaptations   However, Buchner (1930) believes that they have undergone a reduction in both form and function as a result of their symbiotic mode of life According to this view, the simplicity of form is in itself a structural adaptation to symbiotic life

The significance of the phenomena of symbiosis in a study of the relation of insects to the spread and development of disease is quite obvious from the preceding discussion   In many cases of symbiosis with insects, the microsymbiote has proven to be a plant pathogen   With increasing frequency, new cases are being discovered in which insect vectors of important plant diseases maintain some degree of mutualistic symbiosis with the pathogens   The recognition of these interrelations and a thorough understanding of their nature are necessary for intelligently combating the diseases

The investigations by Carter (1933) of the green-spotting disease of pineapples reveal another way in which the micro-symbiotes of insects may be significant in the field of plant pathology   Carter has shown that green spotting is caused by a phytotoxic secretion of the mealy bug and that the toxic secretion is closely correlated with the presence of a rod-shaped symbiote localized in the mycetome of the insect   The increasing recognition of destructive plant diseases caused by toxicogenic insects and the possibility of the toxic secretions being produced by the microsymbiote make it imperative that the phenomena of symbiosis between insects and microorganisms be more thoroughly investigated from this viewpoint

The almost universal occurrence of well-developed mycetomes and microsymbiotes in those insects which are most effective as vectors of virus diseases has suggested the possibility that they may be in some way concerned (Rambousek 1929)   However, no positive evidence of a relationship has been presented and the more recent advances in the study of virus disease give little support to the idea

SELECTED EXAMPLES OF SYMBIOSIS BETWEEN INSECTS AND MICROORGANISMS

Ambrosia Beetles—Schmidberger in 1836 was probably the first to recognize and describe the association of the beetles with the so-called ' ambrosia "   He observed that the beetle larvae fed upon a glistening white substance   He did not understand the fungus nature of the substance interpreted it as a product of the exuding plant sap, and applied the term 'ambrosia" to it   Three years later, Ratsburg (1839) confirmed Schmidberger's observations and suggested that the ambrosia was the product of a mixture of plant sap and insect spittle The fungus nature of the ambrosia was first recognized in 1844 by Thomas Hartig who described the fungus associated with *Xyleborus (Bostrichus) dispar* Fabr in *Alnus cordata* and named it *Monilia candida*   Hartig being a believer in heterogenesis, thought the fungus arose from the wood cells acted upon by a stimulating substance secreted by the beetles

Despite the interesting nature of this association of fungi and beetles, there has been remarkably little study of it   Hubbard in 1897 made what is probably the most extensive study of this

group of insects but made only casual observations of the associated fungi   He concluded, however, that there were more than one ambrosia fungus and that only the most closely related species of beetles have the same fungus for food   Unfortunately, there has been no comprehensive study of the ambrosia fungi   Many casual references and brief descriptions are found in the literature, but no systematic study of the ambrosia fungi has been made   Until quite recently, the name used by Hartig, *Monilia candida*, was the only one applied to this group of fungi   We are indebted to Neger (1908 to 1911) and Schneider-Orelli (1911, 1913), who worked chiefly with species of *Xyloterus* and *Xyleborus*, for the most thorough studies that have been made on any of the ambrosia associations   These investigators have described accurately the fungi associated with the beetles studied and have shown how the fungus is cultivated by the beetles and how it is transmitted from one generation to the next

The true ambrosia beetles belong to the family Scolytidae   They infest a wide variety of trees throughout the tropic and temperate areas of the world and for the most part are found in the wood of trees weakened by some unfavorable condition   They are rarely found in vigorous, rapidly growing trees or in dead ones, although there are some exceptions   They bore deep into the sapwood, each species making its own characteristic brood tunnels   In all cases, the walls are stained a dark color by the associated ambrosia fungus   The tunnels and breeding habits are of two general types   The beetles of one group of genera are semisocial in nature, rearing their young in large communal galleries and sealing dead members of the colony in special death chambers   In the other group, each larva develops in its own separate larval chamber, excavating it as it grows (Fig 25)   In both groups, the chief food of the developing larvae consists of the spores of the ambrosia that fruit in white masses on the surface of the larval chambers   According to Hubbard (1897), the ambrosia fungi associated with these two groups of beetles also are different as indicated by the method of spore formation

The ambrosia fungi invade the wood for only a short distance from the tunnels and apparently do not cause a decay of the wood although the cells adjacent to the tunnels are stained dark brown or black   The fungi live chiefly on the contents of the

cells of the sapwood and do not destroy the cell walls   The value of infested wood is decreased when used for structural purposes, but otherwise the wood is not greatly injured
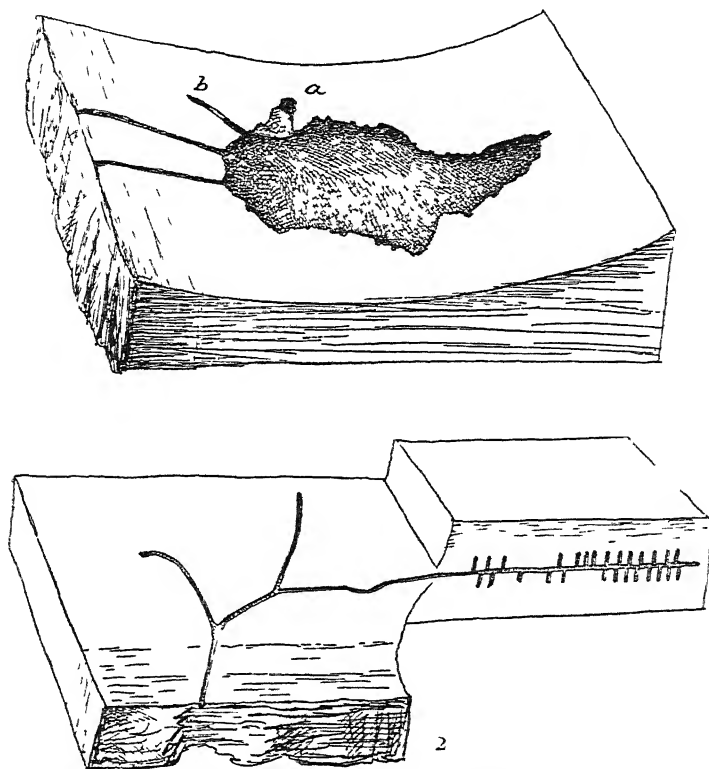
FIG 25 —The two general types of ambrosia-beetle tunnels   1, the communal gallery of *Xyleborus xylographus* in hickory wood *a* and *b*, death chambers or special portions of the tunnels in which dead individuals are sealed off   The ambrosia fungus grows and sporulates over the surface of the entire communal gallery   2 the tunnel of *Monarthrum mali* the type characterized by individual larval galleries   The ambrosia fungus fruits on the surface of the larval galleries   There appear to be two general types of ambrosia fungi corresponding to the two types of tunnel   (*After Hubbard*)

In those genera in which the young are reared in a common gallery, the larvae have mouth parts not suited for chewing wood, and they apparently feed entirely on the fungus   The larvae that develop in individual chambers have strong mandibles that are used to bore out the chamber   In doing this they consume some wood in addition to the fungus   Although

there is no experimental evidence, it is generally assumed that the ambrosia fungi, by concentrating the nitrogenous elements, serve as a supplement to the wood and provide the insects with a more suitable and efficient diet   Other fungi and yeast are often found in the tunnels, but they are suppressed by the beetles so that the ambrosia fungus grows as if in pure culture   As soon as the tunnels are deserted by the beetles, the ambrosia fungus is immediately overgrown by secondary fungi

According to Schneider-Orelli, the ambrosia fungus of *Xyleborus dispar* is transmitted to successive generations in the form of spores in the crop of the female beetle who regurgitates them to start a culture in the new tunnel   Neger, however, thinks the spores are passed through the insect's body and survive in a viable condition in pellets of excrement   Schneider-Orelli states that the spores taken directly from the tunnels of *X dispar* do not germinate, but if recovered from the crop of the female beetle they germinate readily   However, this is not true for all ambrosia fungi   Strohmeyer (1911) has described several species of ambrosia beetles from specimens collected in the tropics in which the female beetles have special chitinous bristles on the front part of the head in which spores and mycelium of the ambrosia fungi are always found   He has interpreted these structures as special organs for the transportation of spores and mycelium of the fungus to be used in establishing cultures in the new brood chambers

Taxonomic studies of the ambrosia fungi are conspicuous by their absence   Neger (1908, 1909) expressed the opinion that the ambrosia fungus of *Xyleborus* is an Endomycete, but neither he nor Schneider-Orelli (1913) reached a final conclusion concerning the identity of the fungus   The fruiting structures of these fungi as they occur in nature are relatively simple, and very few of them have been studied in artificial culture   Trotter (1934) recently reported the study of an ambrosia fungus associated with a beetle of the genus *Xyleborus* found in the wood of *Brownea grandiceps* Jacq in Ceylon   He observed the ' ambrosia'' in material imported into Italy from Ceylon, grew the fungus in several hanging drop cultures, and observed the manner of fructification   In addition to the usual Monilia-like growth, he observed a second layer of mycelium superimposed upon it and forming an abundance of fusiform, hyaline

spores   On the basis of limited observations, he concluded that
the superimposed fungus was a second spore form of the first
For this pleomorphic ambrosia fungus, he established a new
genus *Ambrosiamyces* and named it *A zeylanicus*

Leach, Hodson, Christensen, and Chilton (1940) have recently
reported observations on two species of ambrosia beetles *(Trypodendron betulae* Swains and *T retusus* Lec) found in white birch
(Betula papyrifera) and in aspen *(Populus tremuloides)*, respec-
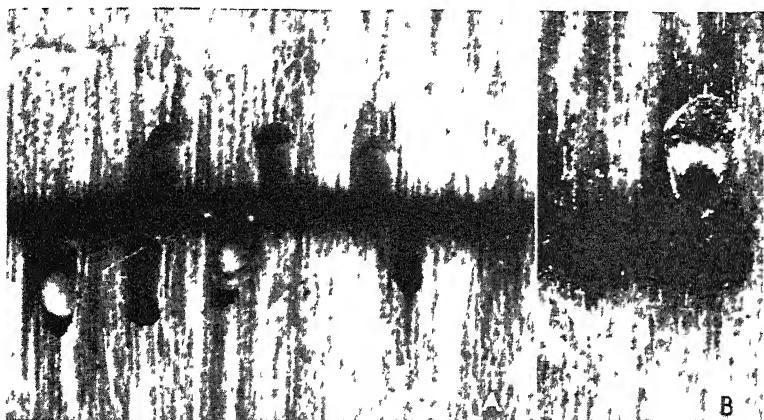
Fig 26 —*A* a section through a portion of a brood gallery of *Trypodendron
retusus* in aspen wood showing the main tunnel blackened by growth of the
ambrosia fungus and several larval chambers arising vertically at right angles
from the main tunnel   The eggs are deposited in small niches in the upper and
lower surfaces of the main tunnel   When they hatch the larvae bore their
tunnels as they grow   The white fruiting layer of the fungus may be seen on the
walls of the larval chambers   Two larvae are shown in their chambers   *B*, an
enlarged view of a small section of an egg gallery and a single larval chamber
showing the white mass of ambrosia fungus consisting largely of spores

tively   These closely related species of ambrosia beetles are
found only in dying trees   They are unable to establish them-
selves in living trees, and dead ones are not attractive to them
probably because of low moisture content   The tunnels are
more abundant near the base of the trees their frequency
gradually diminishing toward the top   The upper limit of
infestation coincides very closely with the lower limit of the
living bark   The life histories and breeding habits of the two
species are very similar

Both species form brood galleries in which the larvae are
reared in individual larval cradles (Fig 26)   In those of *T*

retusus, there is a single entrance tunnel that extends into the wood for a short distance ($\frac{1}{4}$ to $\frac{1}{2}$ inch) and then branches to form two tunnels passing in opposite directions horizontally through the sapwood nearly parallel to the surface   The eggs are deposited in niches on the upper and lower surfaces of the galleries   The galleries of *T betulae* are very similar to those of *T retusus*, but they penetrate more deeply into the heartwood

There is only one brood of the beetles annually   Infestation takes place in May, and the new brood matures in late summer and leaves the trees shortly thereafter   The beetles apparently do not overwinter in the trees, but it is not known where and how they hibernate

The ambrosia fungi associated with these two beetles also are very similar and are in all probability merely strains of the same species   The ambrosia fungus is obviously introduced into the wood by the beetles and may be observed growing on the walls of the tunnels within a few days after the beetles enter the tree   It appears first as a glistening white or cream-colored mycelial growth but rapidly becomes darker, staining the walls a dark-brown color that is almost black   The walls are thoroughly invaded by the brown mycelium, but the fungus does not sporulate extensively in the main gallery   The female beetles deposit their eggs in niches, and each egg is covered with a pad of frass that is always permeated with mycelium of the ambrosia fungus   When platings are made from the frass that covers the eggs, cultures of bacteria, yeasts, and other contaminating fungi are often found but the mycelium of the ambrosia fungus predominates   In a way not clearly understood, the beetles are able to suppress the development of all extraneous fungi so that the ambrosia fungus appears to be growing in pure culture   However, if the beetles are removed from the tunnels, the ambrosia fungus is completely overgrown by other fungi

As the eggs hatch, the young larvae bore out their own cradles, enlarging them as they increase in size   The larvae are oriented with their heads away from the main tunnel, and as they feed upon the wood they enlarge their cradles   The frass is pushed out into the main tunnel, from which it is pushed to the surface by the adult beetles   Almost as soon as the larvae begin to enlarge the egg niche into a larval cradle, the ambrosia fungus begins to fruit on the surface of the walls of the cradle in white,

glistening masses (Fig 26B)   The hyaline unicellular spores
are produced on short, erect sporophores arranged in palisade
layers over the surface of the wood (Fig 27)   These spores
are eaten by the larvae as they enlarge the cradle, but new
layers of spores are repeatedly formed

Prior to pupation, the larvae reverse their usual position in
the cradle and face the main gallery, occupying this position
during metamorphosis, on maturity, the new beetles eat their
way through the plug composed of frass on which the fungus is
usually fruiting (Fig 28)   The beetles thus have every oppor-
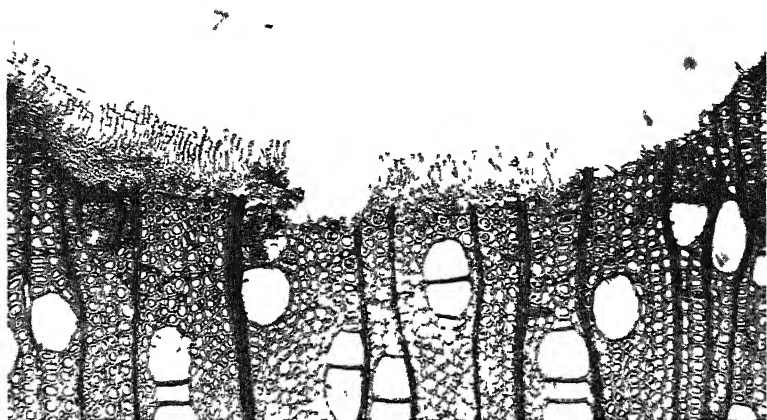
FIG 27 —A cross section of the wood forming the wall of a larval chamber of
Trypodendron betuli showing the palisade layer of sporophores of the ambrosia
fungus   Approx 100×

tunity of becoming contaminated with the ambrosia fungus both
internally and externally before they emerge   The fungus
does not survive metamorphosis within the body of the pupae
The fate of the fungus after emergence and during hibernation
has not been determined

The spores of the ambrosia fungus germinate very erratically
on artificial media, those of the fungus associated with *T betulae*
germinating more readily than the others   Spores produced in
artificial culture germinate more readily than those taken directly
from the tunnels   Both strains of the fungus have been obtained
in pure culture where only minor differences could be observed
The mycelium is hyaline at first, becoming brown with age and
staining the medium brown   At first the fungi sporulate very
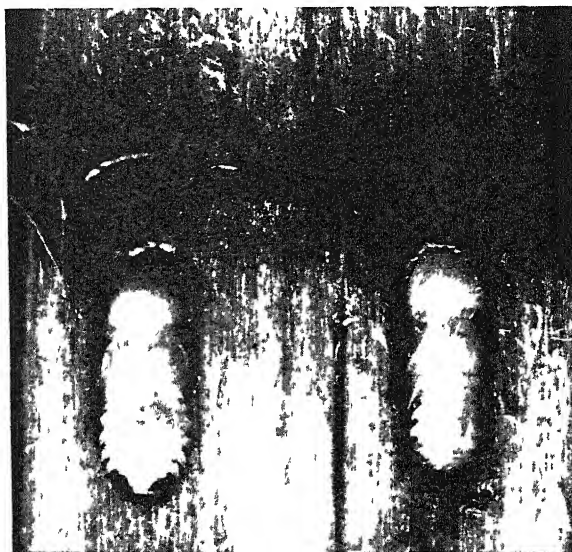
FIG 28 —Two pupae of *Trypodendron retusus* with heads toward the main gallery   Note the white masses of ambrosia fungus growing on the mass of frass separating the pupal chamber from the main tunnel   Approx 8 ×
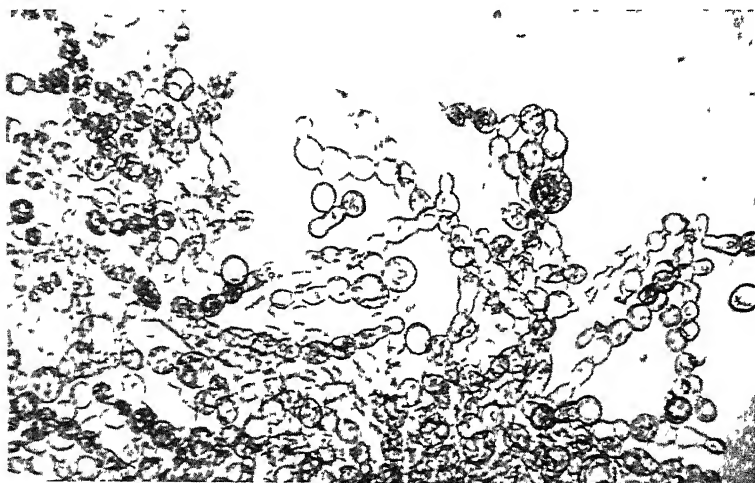
FIG 29 —The ambrosia fungus of *Trypodendron betuli* showing moniliod type of fructification in artificial culture

poorly in artificial culture, forming only imperfect moniloid spores that tend to remain attached and to bud *in situ* White patches and sectors, both of which produced large numbers of hyaline, erect sporophores, later arose on the brown mycelial culture When the patches or sectors were subcultured, a culture that sporulated abundantly was obtained The spores formed in culture are hyaline with thin walls and are ovoid to round They tend to be more spherical than the spores formed in the tunnels (Fig 29) They range from 6 to 17 microns in length and from 6 to 14 microns in width with average dimensions of 11 38 by 10 09 microns The spores are cut off basipetally and the growth of the sporophore is indeterminate

The fungi fall within the range of the genus *Monilia* and, pending more extensive taxonomic studies of the ambrosia fungi, they are considered to belong to the species *Monilia candida* Hartig

Termites and Fungi.—The termites although considered a primitive group of insects, are equal to the ants and the bees in the complexity of their social organization Their extensive caste system, their fungus cultivation and other aspects of their social life have been so well described by Wheeler (1907 1923 and Kofoid *et al* (1934) that only the more significant aspects of their associations with fungi and other microorganisms will be included in the following discussion

Termites are a primitive although ancient, group of insects closely related to the cockroaches They live in highly organized colonies and have a complicated caste system including workers soldiers and reproductives (Fig 30) As a group, they feed largely on cellulose and fungi

The termites fall into two large groups based on their food habits One group feeds primarily on wood and associated fungi, and the other feeds largely on fungi that are cultivated in special fungus gardens in their domatia The wood-eating termites are often extremely destructive to buildings and other wooden structures

The fungus-cultivating termites are confined chiefly to Asia Africa, Australia, and various islands of the Old World They live in large nests, or termitaria, which may be built underground, or in variously shaped, mud-covered structures aboveground (Fig 31) The fungi are cultivated on the excreta of
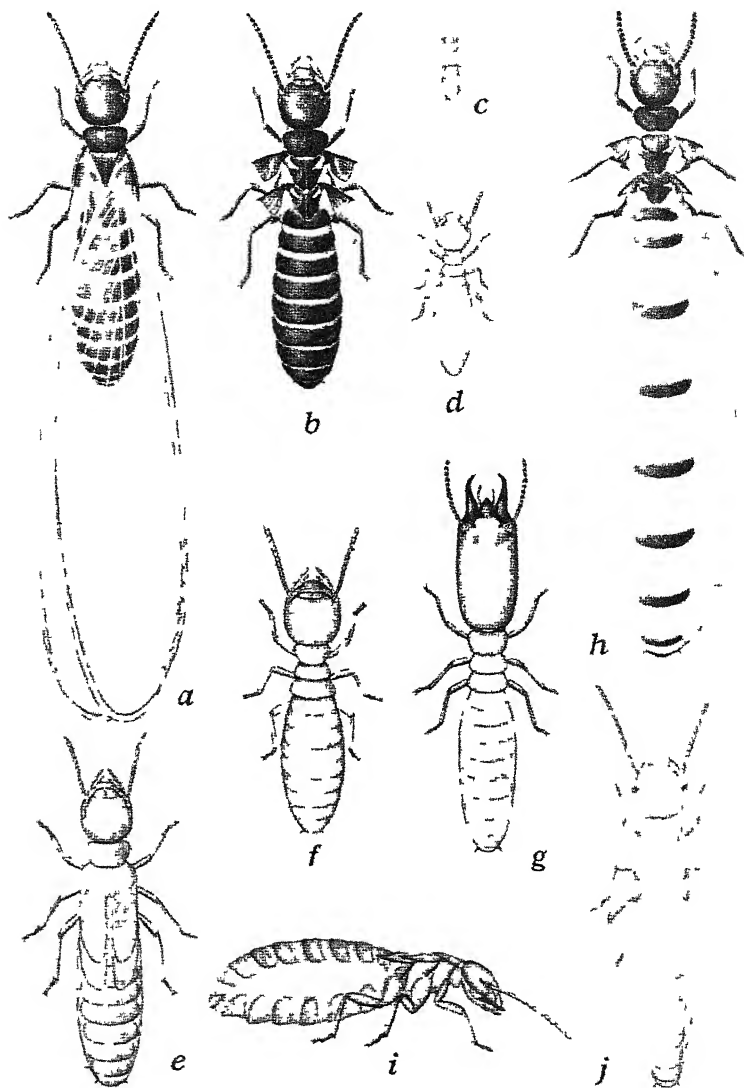
Fɪɢ 30 —The different castes and nymphal stages of the western subterranean termite (*Reticulitermes hesperus* Banks)   a, winged reproductive b dealated reproductive, c a very young nymph caste not yet evident, d, third-instar nymp, caste not evident e, late nymph of reproductive caste, f, mature worker caste, g, mature soldier caste h, mature breeding queen, ι, short-winged brachypterous, or second-form individual of the reproductive caste, called a 'supplementary reproductive'' ɟ, wingless, apterous, or second-form individual of the reproductive class, also known as a supplementary reproductive   (*After Kofoid et al*)

the termites in special compartments of the termitarium   The spores of the fungus are ingested by the termites, are passed uninjured through the intestinal tracts of the workers and thus are introduced automatically into the substrate   The fungus is used almost exclusively as food for the young and for the royal

FIG 31 — A termitarium of the Philippine mound-building termite *Macrotermes gilvus* cut open to show the spongelike fungus gardens   (*After Kofoid et al*)

castes   The soldiers and workers do not feed upon the fungus but use other plant material

Very little is known about the identity of the fungi cultivated by the termites   Fruiting bodies of Xylaria and Volvaria have been found associated with the gardens and are thought by some to be identical with the fungi in the gardens   However, very few of the fungi associated with the termites have been

studied extensively, and more careful taxonomic studies are desirable

Many species of termites that do not cultivate fungi in special gardens feed on wood decayed by fungi Others are able to destroy healthy wood, but it has been observed that the wood adjacent to the tunnels made by the termites is always infested with fungi This suggested the possibility that even these species might be more closely associated with fungi than previously supposed Accordingly, Hendee (1933) has made a study of the association of fungi with three species of termites [*Kalotermes minor* (Hagen), *Reticulitermes hesperus* Banks, and *Zootermopsis angusticollis* Hagen] that are destructive to buildings Hendee isolated 33 known genera and 20 nonsporulating cultures of fungi from the termites or their burrows *Penicillium* and *Trichoderma* were the genera most constantly present, but there was no evidence of a specificity of association as the same species are found in nature independent of termites The termites however, are never found without the fungi There was no correlation between the fungi present and the species of wood attacked by the termites It was shown that the termites regularly transported viable spores into locations to which they would not have access otherwise and that the fungi invaded the wood a short distance ahead of the excavations of the termites The fungi associated with some termites (*Reticulitermes* and *Zootermopsis*) causes a definite wood decay

In a further series of nutritional experiments with *Z angusticollis,* Hendee (1935) has shown that the fungi play an essential role in the natural diet of the termites This was done by feeding the termites on various fungus-containing and fungus-free diets and measuring the effects of each by several different criteria In interpreting the role played by fungi, Hendee states

The fungi offer a source of proteins They probably supply vitamins which are essential to the normal growth and development of termites Through the secretion of extracellular enzymes they may render the wood itself more available It is not known what effect the fungi may have on harmful extractives of the wood

Termites and Protozoa.—A discussion of the symbiotic life of termites would not be complete without a brief consideration

of the symbiotic protozoa and the part they play in the nutrition of these insects   It is now known that practically all species of wood-eating termites harbor in their intestinal tracts large numbers of protozoa   The significance of these symbiotic protozoa has been studied extensively by Cleveland (1923 to 1934) who proved experimentally that they are necessary for the digestion of the cellulose of the wood on which the termites feed   Cleveland (1924, 1925*b*, 1925*c*) found that the termites could be freed of protozoa by subjecting them to high temperatures (24 hours at 36 degrees centigrade) or by oxygenation Such defaunated termites died of starvation within 10 to 20 days if kept free of protozoa, but if recontaminated with the protozoa of their normal intestinal fauna, they continued to live and develop normally   Mansour (1934*b*) has questioned Cleveland's conclusions and adduces evidence to support the view that the relationship is not mutualistic symbiosis but one of commensalism, in which both termites and protozoa get all their required food from the wood and derive no benefit from the association However, the more recent work of Hungate (1936 1938) supports the conclusion that the protozoa are essential in the digestion of cellulose   This author has made extensive quantitative studies of wood digestion in faunated and defaunated termites (*Zootermopsis nevadensis* and *Z angusticollis*)   He concludes the protozoa are responsible for digesting approximately two-thirds of the total amount of wood that is utilized and that the remaining one-third is available without the aid of the protozoa The latter quantity, however is not sufficient to meet the energy requirements of the termites, which is shown to be seven-eighths of the total amounts of wood digested by all agencies

Cleveland (1925*a*, 1928) cultivated reproductive colonies of termites for more than 18 months on a diet of filter paper and concluded that they could live indefinitely on a diet of pure cellulose although he was at a loss to account for the source of nitrogen required for their fortyfold increase in weight   He concluded that ''they must be able in some way to fix atmospheric nitrogen which they use in manufacturing proteins or else, contrary to the current opinion they must be able to transform carbohydrates into proteins ''   He was unable to demonstrate fixation of atmospheric nitrogen, and as the other alternative is obviously impossible the question of the source of nitrogen was

left unanswered   Cook and Scott (1933) have questioned the ability of termites to survive on a diet that includes carbohydrates, proteins salts, and vitamins A, B, D and G   These authors used as criteria the viability and the group weight of nonreproductive colonies over a relatively short period of time and placed considerable weight on the presence or absence of cannibalism   These criteria are subject to some criticism because as pointed out by Hendee (1935) cannibalism often occurs in normal colonies on a natural diet of rotten wood   This might account for a decrease in weight and numbers during the first few months that could not be attributed to a deficient diet   Even though the termites may not be able to survive indefinitely on a diet of pure cellulose as claimed by Cleveland, his data indicate that the colony lived and thrived for a surprisingly long time on a diet of pure cellulose

Uvarov (1928) in discussing the nutrition of termites, commented "The most difficult problem is not the digestion of cellulose but how to discover the means by which the deficient nitrogen is obtained   The only suggestion made in this direction is that symbiotic microorganisms are able to fix atmospheric nitrogen but there is no evidence of any kind in support of this theoretically very reasonable view "

A possible explanation of the apparent ability of termites to thrive on a nitrogen-deficient diet has been offered by Leach and Granovsky 1938)   The hypothesis is based on a possible nitrogen cycle within the termite colony   The symbiotic microorganisms including protozoa, bacteria and spirochetes, are localized in an enlargement of the hind-gut *posterior* to the point where the Malpighian tubules enter the intestinal tract (Fig 32)   The urates and other nitrogenous waste products excreted by the Malpighian tubules are probably utilized as food by the microorganisms and elaborated into protoplasm   Since proctodaeal or anal feeding (the feeding on excreta of other individuals) is common among termites the bacteria and protozoa or their dead bodies obviously are consumed by some individuals of the colony   Refaunation has been considered the principal function of anal feeding   It may also play a part in the nitrogen economy within the termite colony   The synthesis of protoplasm from urates by the protozoa and the utilization of the dead protozoa as food by the termites would permit the same nitrogen supply

to be used over and over   In this way, the metabolic processes
of the termite colony could continue indefinitely as long as
carbohydrates were available   The maximum size of the colony
would of course, be limited by the amount of nitrogen originally
available in the bodies of the founders of the colony   Within
this limit, such a nitrogen cycle within the termite colony would
permit the colony to live for a very long time on a diet apparently
consisting of cellulose only
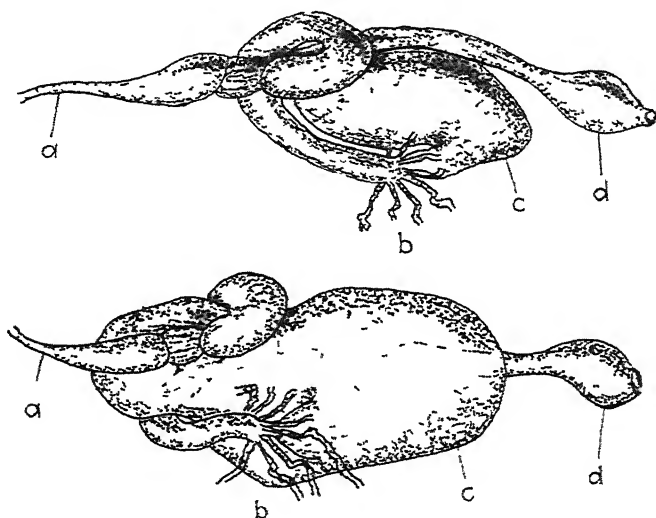
Fig. 32 —Intestinal tracts of worker and soldier castes of *Calotermes flavi-
collis* Fabr   *a*, oesophagus, *b*, *Malpighian tubules*, *c*, enlarged port on of hind-
gut in which protozoa are localized, *d* rectum   Note that the enlargement
containing the protozoa is behind the point of entrance of the *Malpighian tubules*
(*Redrawn from Buchner's "Tier and Pflanze in Symbiose," by permission of
Gebruder Borntraeger*)

It is also probable that some nitrogenous matter derived from
dead protozoa within the digestive canal is absorbed directly
through the anterior region of the hind-gut   Child (1934)
in a study of the internal anatomy of termites concluded that
some portion of the voluminous organ formed by the vestibule
large intestine, and caecum must absorb the digested food
material   This organ with its large expanse of thin walls is
bathed by the hemolymph and is excellently suited to the
purpose   The conclusion is supported also by the fact that the

wood particles are not completely digested until they reach the hind-gut   If nitrogenous compounds derived from the dead protozoa are absorbed in this region, the nitrogen is probably used over and over by a single individual, thus increasing greatly the efficiency of the insect's nitrogen economy

Termites appear to have developed a highly effective method of conserving nitrogen   In all probability, the fungus-cultivating
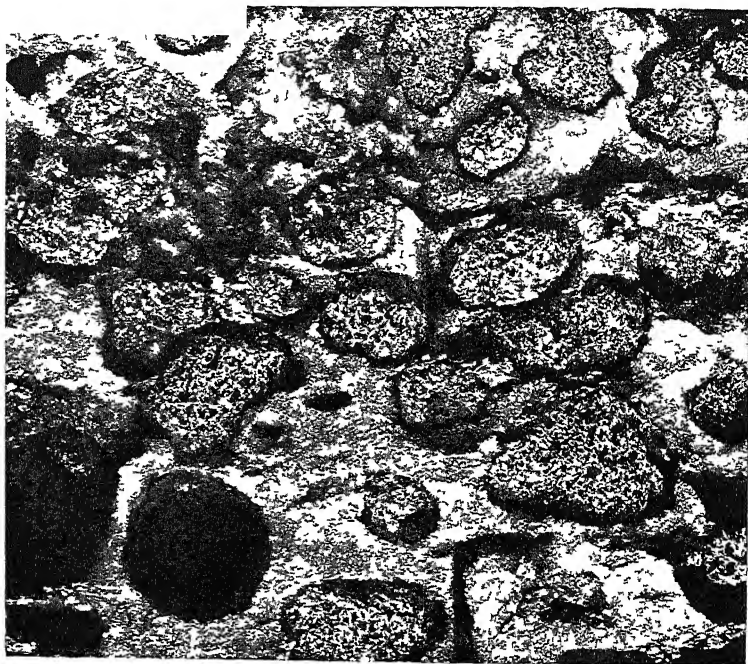
FIG 33 —A sectional view of a portion of a nest of the fungus-cultivating ant *Atta vollenweideri* showing the chambers containing the spongy fungus gardens (*After Wheeler, with permission of Harcourt, Brace & Company*)

habit of termites is also based on a similar nitrogen economy It is well known that the fungi cultivated by the termites grow almost exclusively on the excreta   The fungi transform nitrogenous waste products into fungus protoplasm, which is in turn consumed by the termites to form more excreta on which to grow more fungi

Ants and Fungi.—Ants are among the most highly developed insects, and, according to Wheeler (1923), "the number of individual ants is probably greater than all other insects "

They are highly social in their life habits   The leaf-cutting ants and the fungi that they cultivate constitute one of the best examples of ectosymbiosis of insects and fungi   Other species of ants are often associated to a lesser extent with fungi, and a few species have been suspected of being vectors for plant pathogenic fungi   Wheeler (1907, 1923, 1937) and Weber (1937, 1938) have given such a full account of the biology of these ants and their associated fungi that only the briefest outline will be given here
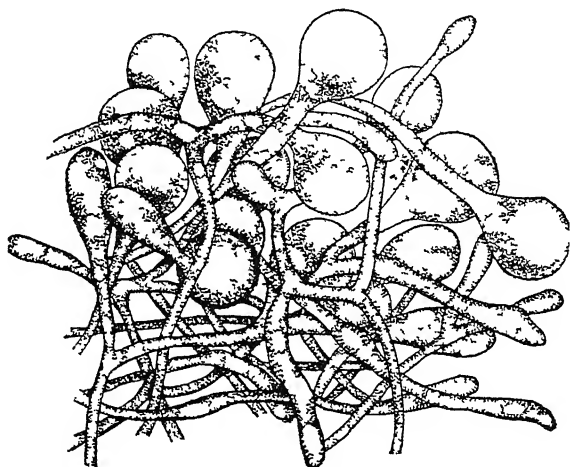
FIG 34 —"Bromatia" or globular swellings of the hyphal tips of the fungus cultivated by ants   The ants feed upon the bromatia in preference to the normal mycelium   *(From Wheeler after Carlos Bruch, with the permission of Harcourt, Brace & Company)*

The fungus-cultivating ants consist of about a hundred tropical or subtropical, exclusively American species belonging to the tribe Attini   These ants live in enormous colonies in extensive underground nests   They forage on all kinds of vegetation for long distances in every direction   Leaves and other succulent plant parts are cut and transported into underground nests where they are used as a substrate for the cultivation of the associated fungus   The plant fragments are worked into a spongy pulp on which a luxuriant fungus growth is maintained (Fig 33)   A different fungus appears to be cultivated by each species or group of closely related species of ants

As the fungi grow in the "gardens," no spores are formed, but characteristic club-shaped hyphal tips composing the so-called "bromatia" are produced in abundance   The bromatia constitute the edible portion of the fungus, and, as the swollen ends are eaten, new ones are constantly formed (Fig 34)
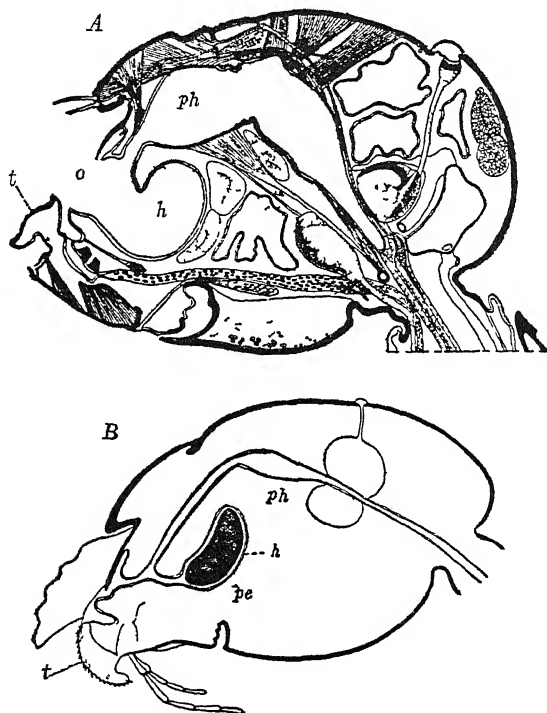
Fig 35 —Saggital sections through the ant head showing the infrabuccal pouch and pellet   A a queen of *Lasius niger* with the mouth open, *B*, a queen of *Componotus brutus* with the mouth closed, *t*, tongue, *o*, oral orifice, *ph*, pharynx, *h*, infrabuccal pouch, *pe*, infrabuccal pellet   (*After Wheeler, with permission of Harcourt, Brace & Company*)

The identity of the cultivated fungi has not been determined definitely, but the fruiting bodies of certain Agarics and of Xylaria have been found associated with the fungus gardens Moller in 1893 described an Agaric found associated with the nests of *Acromyrex disciger* Mayr and named it *Rozites gongylophora*   Spegazzini in 1899 found a stroma growing from the nest of *Acromyrex lundi* and named it *Xylaria micrura*   Bruch (1922), also, has reported this fungus associated with the same

species of ant   Wheeler (1907) described a yeastlike fungus cultivated by *Cyphomyrmex comalensis*, named it *Tyridiomyces formicarum*, and placed it among the Exoascaceae, although no ascospores were observed   These papers and others dealing with the identity of the ant-cultivated fungi are reviewed by Weber (1938) who has also described *Lentinus atticolus* Weber as the fungus cultivated by *Atta cephalotes* L

The technique of cultivation of the fungi by the ants has been described in detail by Wheeler (1923)   When the ants swarm and new colonies are established, the female retains a mass of the fungus and leaf tissue, or "spawn," in her infrabuccal pouch (Fig 35)   After mating and burrowing into the soil, this spawn is used in starting a new fungus garden   Fresh leaf tissue is added to the spawn, and the new garden is fertilized with excrement and often with eggs which are crushed and mixed with the substrate (Fig 36)   The garden is later cared for by the workers, and the larvae feed exclusively on the bromatia

There is a striking similarity between the fungus-cultivating habits of the ants and of the termites   Both cultivate their fungi in special fungus gardens on an organic substrate   The termites utilize their excrement as a substrate for the fungi while the ants prepare a special substrate of plant tissue   The fungus gardens of the ants growing on the substrate, however, are constantly fertilized by excreta, and Weber considers "that the role of the substratum is largely passive, affording mainly a convenient framework for the nutritive fecal droplets and the mycelium which grows on them   A cycle is thus set up which is theoretically endless, the ants feeding on a fungus which in turn grows on the excrement of the ants "

The infrabuccal pouch, an organ characteristic of ants, is an interesting structure and demands further consideration from the standpoint of fungus associations   This pouch (Fig 35) is used by ants in general as a screen and repository for particles of solid material not suitable for ingestion   When the pouch has become filled, the contents are discharged in the form of pellets which often contain, among other things, large quantities of fungus spores as shown by Bailey (1920) (Fig 37)   He worked with specimens preserved in alcohol and did not determine the viability of the spores taken from fresh pellets   Germination experiments reported by Leach and Dosdall (1938), however,
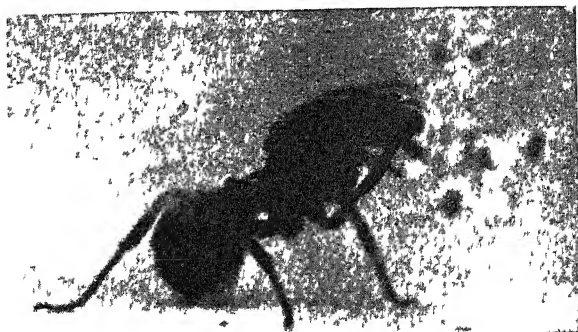
FIG 36 —Photographs showing a queen ant (*Moellerius heyeri*) *A*, in the act of laying an egg, *B*, placing an egg in the fungus garden, *C*, in the act of fertilizing the fungus garden by defecation   (*After Wheeler, with permission of Harcourt, Brace & Company*)

show that some of the spores in the infrabuccal pellets of *Formica
fusca* var *subserica* Say are viable   Because ants are constant
visitors to all parts of plants, both diseased and healthy, these
observations are of considerable significance   Ants found con-
stantly associated with a fungus plant disease should be viewed
with suspicion   Although ants have not been incriminated as
vectors of plant pathogens in many instances, there are a few
cases on record   For example, Dade (1927) has reported that
ants are important vectors of the mealy-pod disease of cocoa
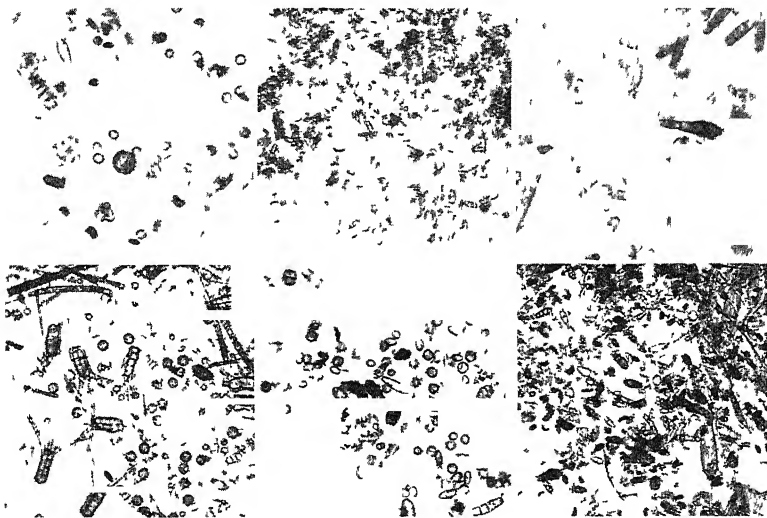
Fig 37 —Photomicrographs showing the fungus spores found in the infra-
buccal pouches of six different ants   The pellets were dissected out, crushed in a
drop of water on a slide, and photographed   (*After Bailey*)

in the African Gold Coast   This disease is caused by a Phy-
comycetous fungus (*Trachysphaera fructigena*), which forms
masses of spores on the surface of affected pods   Ants regularly
feed upon the diseased pods, and they were observed transporting
the spores   The ants were considered effective agents of spore
dissemination, although it was recognized that the spores may
also be scattered by wind and rain

There is still another way in which ants may be involved
indirectly in the transmission of plant diseases   It is well
known that many species of ants utilize as food the so-called
"honeydew" of aphids and other homopterous insects   The

honeydew is in reality the excrement of these insects and is sought by the ants because of its high sugar content   The plant juices ingested by the aphids and scale insects have a high water and sugar content in relation to proteins   In order to obtain the required amount of protein food, an excess of water and sugar must be ingested   This excess is voided in the form of the sugary solution known as honeydew   Many species of ants have acquired the habit of caring for aphids, mealy bugs, and other insects so that they may utilize the honeydew to the best advantage   Individual aphids, for example, are transported by ants from plant to plant and placed in the proper location for the establishment of colonies   Some ants even collect the aphid eggs in the fall and preserve them in their nests over winter   So highly specialized is this relationship that Linnaeus referred to aphids as the "dairy cattle of the ants"   As aphids are the most common vectors of virus diseases, it is evident that the association is one that should not be overlooked in the study of insect transmission of virus diseases and of the control of the insect vectors

Ants that attend the pineapple mealy bug [*Pseudococcus brevipes* (Ckl)], a toxicogenic insect causing a destructive wilt of pineapple, are essential for their normal development, according to the work of Carter (1933*a*)   No successful attempts to control aphids or mealy bugs by controlling the ants have been reported   Unfortunately, effective control of the ants often is more difficult than direct control of the aphids or mealy bugs

Septobasidium and Scale Insects —Couch (1931, 1939) has described in considerable detail a unique case of mutualistic symbiosis between the fungus, *Septobasidium burtii* Lloyd, and a scale insect, *Aspidiotus osborni* New and Ckl   *S Burtii* is a well-known Basidiomycete occurring on the branches of many kinds of trees (Fig 38)   Although the injury to the tree is slight, the fungus has been considered by some to be a parasite   Others have held it to be an epiphyte, and still others have considered it a saprophyte living on the excretions of the scale insects   Couch has demonstrated that the fungus and the scale insects live symbiotically at the expense of the host plant   The scale insects live among the folds of the fungus where they are protected against enemies and unfavorable environment   In this home furnished by the fungus, the scale insects suck the

juices from the host plant, grow, and multiply   In return, the insects supply nourishment for the fungus   The mycelium of the fungus penetrates the body cavities of a number of the insects and forms numerous coillike haustoria   The nourishment absorbed from the insects through these haustoria supports the growth of the fungi   The fungus is disseminated entirely by young insects that become infected with the fungus and migrate
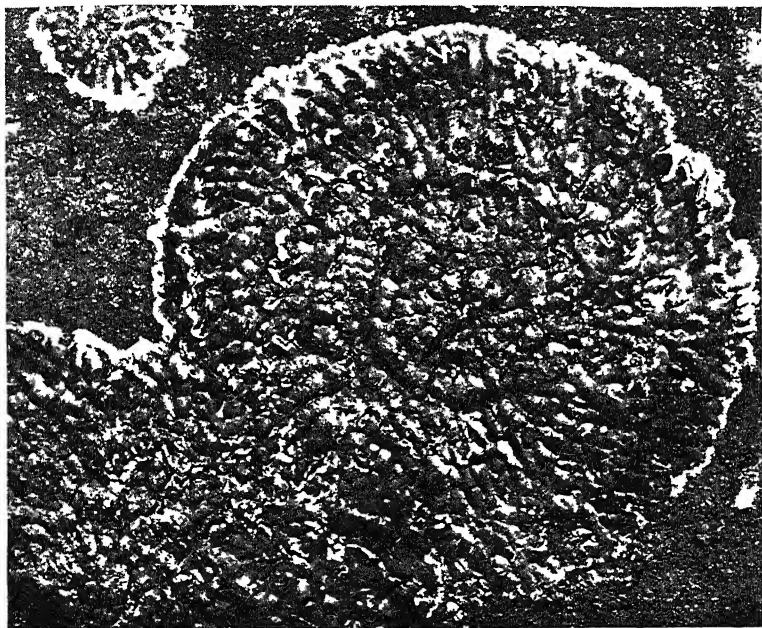
Fig 38 —*Septobasidium Burtii* growing on the bark of *Quercus palustris* Surface view showing the radiating ridges and depressions that mark the openings to tunnels occupied by the scale insects   Approx 4 ×   (*After Couch, by permission of University of North Carolina Press*)

to new localities   Unless the insects are infected when young, they remain free of the fungus, for the older ones are immune to infection   Some individual insects die and are absorbed by the fungus, others apparently digest the fungus haustoria, and others are free from infection   In Fig 39 is reproduced Couch's diagrammatic representation of this symbiotic relationship Similar symbiotic structures, varying with the species of fungus and insect, have been reported by Couch

This symbiotic association appears to be universal in the genus *Septobasidium*   Couch (1935, 1939) has demonstrated it for

Fig 39 — A diagrammatic representation of the symbiotic association of the fungus *Septobasidium burtii* and the scale insect *Aspidiotus osborni*   The insect derives protection from the fungus, and the fungus derives its food by parasitizing some of the insects   (*After Couch, by permission of the University of North Carolina Press*)

at least 33 different species   Some species of *Septobasidium* are associated with only one species of scale insect while others may be associated with several species   In general, those species

of *Septobasidium* occurring on a wide variety of host plants are more likely to be associated with several species of scale insects

Bacteria and Dipterous Insects —That type of endosymbiosis in which the microsymbiote lives in the lumen of the intestinal tracts or in intestinal diverticula is well illustrated by the symbiotic relations between dipterous insects and bacteria, many of which are involved in destructive plant diseases Several of these insects and their symbiotic relationships, including the seed-corn maggot, the apple maggot, and the olive fly, are described in detail in Chap VI

The Drugstore Beetle and Symbiotic Yeast —This is the best-known example of endosymbiosis in which the microsymbiote has become intracellular and is found in mycetocytes in the intestinal wall or in the walls of intestinal caeca The relationship between the drugstore beetle (*Sitodrepa panicea* L) and its symbiotic yeast has been studied extensively by Buchner (1921) This beetle feeds on a variety of food materials, especially dried plant and animal products Digestion of the food materials is accomplished through the aid of a symbiotic yeast (*Saccharomyces anobii* Buchner) that is closely and constantly associated with the intestinal tract, being found in the lumen and also in the epithelial cells of the larval intestine as well as in the cells of special caeca in the imago The yeast is transmitted from generation to generation through surface-contaminated eggs The microsymbiotes are found in great numbers in two intersegmental pouches, from there, they are discharged into two vaginal pockets from which they reach the eggs in the process of oviposition (Fig 40) The eggs, as they are laid, press against the pockets and become surface-contaminated with the yeast When the eggs hatch, the larvae become contaminated from the yeast cells adhering to the surface of the egg shells

Intracellular Symbiosis in the Homoptera —Intracellular symbiosis reaches its highest development in the Homoptera where the condition is practically universal The microsymbiotes are found deep in the body tissues either free in the hemolymph or in individual mycetocytes or in mycetomes Symbiosis of this type has been rather extensively investigated by Pierantoni, Sulc, and Buchner Brain in 1923 summarized the literature to that date and drew up a provisional classification

of the described microsymbiotes, establishing a number of new genera   The generic names for these microsymbiotes living free in the hemolymph or connective fat tissue were formed by combining the suffix "cola" with some other descriptive word, usually the genus or class name of the insect   For those microsymbiotes constantly inhabiting definite mycetocytes or myce-
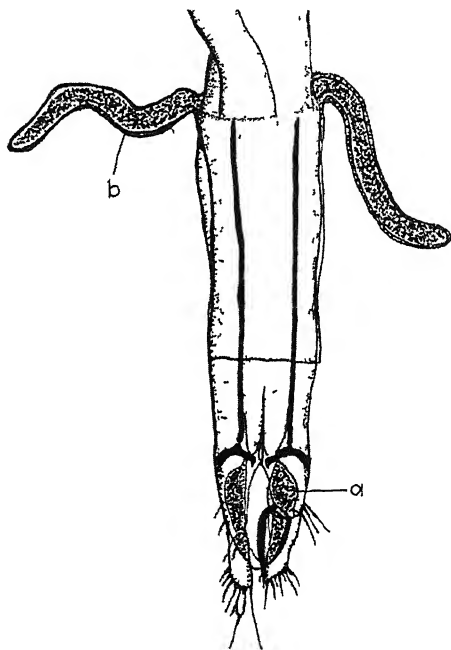
Fig 40 —The ovipositor of *Sitodrepa panicea* showing the vaginal pouches (*a*) filled with symbiotic yeast cells that contaminate the eggs at time of oviposition, and the long intersegmental pouches (*b*) in which a constant supply of the yeast cells are maintained   (*After Breitsprecher, from Buchner's "Tier und Pflanzen in Symbiose" with permission of Gebruder Borntraeger*)

tomes, the suffix "myces" is used   Thus, *Lecaniocola, Cicadocola,* and *Cicadomyces, Aphidomyces,* etc   Forty-two species of microsymbiotes belonging to 13 genera were described

A typical representative of this type of symbiosis has been described in some detail by Granovsky (1929) who studied the intracellular symbiotes of *Saissetia oleae* (Bernard) taken from oleander plants growing in a greenhouse   The yeastlike symbiote (Fig 41*a*) was found constantly associated with all stages in the

development of the insect, although they were more abundant in half-grown nymphs and in young females   No similar organism was found on the leaf surface, in the honeydew secreted by the insect, or elsewhere outside the insect body   The microsymbiote was not grown in artificial culture, but it was seen to multiply by budding during the first 24 hours when suspended in a hanging drop of normal salt solution

Histological studies showed that the microsymbiotes occurred free in the hemolymph as well as in the cells of the connective fat tissue   As the amount of fatty tissue decreases, in mature females, the microsymbiotes decrease in abundance, probably by death and disintegration   The association of the micro-
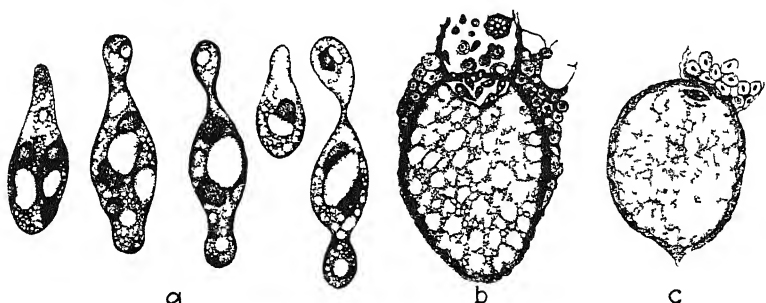
FIG 41 —*Lecaniocola saissetiae* the yeastlike symbiote of *Saissetia oleae*   *a*, the symbiote showing multiplication by budding in a normal salt solution within 24 hours after removal from the insect, *b* and *c*, the symbiotes invading the developing egg from the nurse cells   (*After Granovsky*)

symbiotes with the fatty tissues has suggested that they may aid in the digestion of the reserve foods during the reproductive life of the insect   Congenital transmission is accomplished by internal infection of the eggs   This apparently occurs through the anterior end of the egg through the nurse cells (Fig 41*b*) or by direct penetration near the anterior pole   The organism was described and, following Brain's system of nomenclature, named *Lecaniocola saissetiae*

Perhaps the most highly specialized type of symbiosis of this kind is represented by that found in the Aphididae   All members of this family are equipped with a large mycetome divided into two longitudinal halves   This structure was first observed and described by Leydig in 1850 and was further studied by Huxley (1859), who applied the name "pseudovitellus" to it   Pierantoni

(1909, 1910) and Sulc (1910) were the first to demonstrate the presence of symbiotic microorganisms in the structure, Sulc introducing the terms "mycetome" and "mycetocyte" The most recent and most exhaustive study of the mycetome of the Aphididae is that of Uichanco (1924), who has described in detail the method of congenital transference of the mycetome and the included symbiotes The follicular epithelium becomes infected by the symbiotes during the early stages of development and harbors them in a dormant condition During the earlier cleavage stages of the egg, the dormant symbiotes come in contact with the egg yolk and are stimulated to rapid multiplication As a result of the growth of the symbiotes, there is a swelling of a portion of the follicular epithelium, the symbiotes break through the thin epithelial cells, invade the posterior portion of the egg cavity, and appropriate the yolk mass enclosed there In this way, every individual receives its complement of mycetocytes and the associated microsymbiote

After birth of the aphid, the mycetocytes cease to multiply but increase to approximately double their original size The symbiotes, however, multiply extensively As the insect reaches maturity, the mycetocytes begin to degenerate until the death of the insect, when only a few are left

The mycetome is present in every individual aphid, both male and female, regardless of method of reproduction This constant association of the microsymbiotes would indicate that they play an important role in the biology of the aphids, but their function is still an unanswered question

Rickettsia —This name is applied to a group of very small bacterialike microorganisms that are found living symbiotically in the alimentary canal of many insects and other arthropods They are found frequently within the epithelial cells where they apparently cause no injury although some workers consider them parasitic instead of symbiotic They also may invade other tissues, including the salivary glands from which they enter the salivary secretions Moreover, most of them appear to be congenitally transmitted to successive generations through the eggs Rickettsia are Gram-negative and stain poorly with aniline dyes but take the Giemsa stain readily They are usually less than half a micron in diameter It is extremely difficult if not impossible to cultivate them in artificial media

A number of Rickettsia are pathogenic to animals, causing such diseases as typhus fever, the Rocky Mountain spotted fever, and trench fever The generic name Rickettsia was first used to designate the pathogen of typhus fever (*Rickettsia prowazekii*) This binomial honors Ricketts and Prowazek, two investigators who died of typhus fever while investigating the disease The pathogenic Rickettsia are all transmitted by arthropods and are adapted to alternate existence in arthropods and in higher animals

Swezy and Severin (1930) have reported Rickettsia-like microorganisms in the epithelial cells and lumen of the intestines of the sugar-beet leaf hopper (*Eutettix tenellus*) These workers suggested a possible relationship of the Rickettsia-like organisms to the cause of curly top of sugar beets There is, however, no convincing evidence that the microorganisms are concerned in causing the disease No plant parasitic Rickettsia are known

In the preceding discussion, it has been possible to touch only briefly upon a few of the most important aspects of the subject of symbiosis between insects and microorganisms The subject is extremely complicated, and although a large body of information has accumulated in recent years, the principles underlying the phenomenon are only imperfectly known Relatively little accurate information is available on the physiological bases of symbiosis, and the biological significance of the associations is not well understood It is evident, however, that symbiosis between insects and microorganisms is a relatively common phenomenon and that such associations are often directly concerned in the spread and development of plant diseases For these reasons, it is obvious that the subject should not be neglected by anyone interested in insects as vectors of plant pathogens

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CHAPTER IV

THE RELATION OF INSECTS TO THE SPREAD AND DEVELOPMENT OF PLANT DISEASES

HISTORICAL

The parasitic nature of the most common plant diseases was not recognized until the middle of the nineteenth century. Prior to this time, the autogenetic theory of the cause of plant diseases prevailed. Fungi were known to be associated with the diseased plants, but they were thought to be a result of the disease rather than the cause. For example, such parasitic fungi as the rusts and smuts were visualized as products of the disordered sap of the diseased plants. The spores of these fungi had been seen through the microscope, but it was not known that they could germinate and infect healthy plants. It is only natural that few or no significant observations concerning the role of insects in the spread and development of plant diseases were made until the true nature of parasitic plant diseases was recognized.

The publications of De Bary, beginning in 1853, proved conclusively the parasitic habits of fungi associated with diseased plants. De Bary's work and that of his contemporaries, Julius Kuhn and the Tulasne brothers, changed the whole concept of the nature and cause of plant diseases. During this period, Pasteur and Koch proved and established the germ theory of animal diseases, and in 1881 Burrill demonstrated, for the first time, that bacteria could cause plant diseases. These fundamental discoveries greatly stimulated the study of both plant and animal diseases, and rapid advances were made. At first the greatest emphasis was placed on the discovery and proof of the causes of the various diseases. Many new microorganisms were found and described, and their pathogenicity was proved. Later, attention was turned to the means of spread and to the factors influencing the development of diseases. It was then that pertinent observations and experiments on the role of

insects were made   This does not mean that the idea of insect transmission of diseases did not appear until the parasitic nature of diseases was recognized   Indeed, there are numerous early references to the subject and expressions of opinion that insects were concerned in the development of diseases of both plants and animals   Some of these theories were based on careful observation and bore some elements of truth   Many of them, however, were imaginary and inaccurate, and none of them received much credence at the time   It was only after later experimentation had established the real nature of the relationships that those earlier observations, which were so near the truth, appeared significant   A classic example is that of the Italian physician Mercuriales, who, in the sixteenth century, formulated a theory that the plague (Black Death) was spread by flies   He held that the disease was transmitted by flies feeding upon excretions of diseased individuals and later defecating upon human food   Although his theory was not based on experimental evidence and was incorrect, it is nevertheless based upon a concept of the infectious nature of diseases that was not fully appreciated until 250 years later

The first experimental proof of insect transmission of a plant disease was reported in 1891 by Waite, who showed that bees and wasps, while visiting pear blossoms in search of nectar, were active vectors of the bacteria causing fire blight of pears Seven years earlier, Forbes (1884) had observed the tarnished plant bug feeding on blighted pear twigs and had expressed the opinion that the insects transmitted the disease from tree to tree   No experimental proof was offered by Forbes, but the correctness of this theory was verified by Stewart (1913) nearly thirty years later

The proof that the troublesome fire-blight disease was disseminated by bees and other insects served to focus the attention of plant pathologists on the problem   Although Waite's work was not extensive and he left many pertinent questions unanswered, he experimentally transmitted the disease by means of bees from one blossom cluster to another and protected other blossoms from infection by caging them and excluding the insects He demonstrated the presence of the pathogen in and on the mouth parts of bees and wasps caught in the orchard   Even though the work was fragmentary and incomplete, it marks the

beginning of experimental investigation of insects in relation to plant diseases and has furnished the necessary stimulus for further study

In 1901, Takami, working in Japan, showed that the dwarf disease of rice, now known to be a virus disease, was brought about as a result of the feeding of a leaf hopper (*Nephotettix apicalis* Motsch) This was a discovery of funadmental significance, but partly because the work was published in the Japanese language, it was generally overlooked until other investigators working with similar diseases had demonstrated that virus diseases were generally transmitted by insects In fact, according to Katsura (1936), Takami in 1901 did not have the concept of the leaf hopper acting as a vector of an infectious disease but rather considered the insect as the sole cause of the disease Only after several years of subsequent work was the correct nature of the relationship realized and published in 1908 and 1909 in the reports of two Japanese experiment stations

Ball, in 1906, five years after the publication of Takami's paper, demonstrated that curly top of sugar beets was associated with the leaf hopper [*Eutettix tenellus* (Baker)] The subsequent work of Shaw (1910), Smith and Bonquet (1915), and others soon demonstrated the infectious nature of the disease and the true role of the leaf hopper as a specific vector of curly top At about this time, Allard (1912) showed that a virus disease of tobacco was transmitted by aphids These discoveries of Ball and Allard marked the beginning of a long series of investigations that has shown the great importance of insects as vectors of a large number of virus diseases They opened up a new and fruitful field of research

Similar developments were being made in the field of animal pathology at approximately the same time that plant pathologists were recognizing insects as important vectors of plant diseases As early as 1878, Manson had shown that mosquitoes were the vectors of *Filaria bancrofti*, the nematode worm causing elephantiasis of man This early discovery of the transmission of a disease of man by an insect had a profound influence on the trend of development in medical science Manson, convinced of the potential significance of mosquitoes as vectors of disease, stimulated and encouraged Ross in his classic studies on the transmission of malaria by mosquitoes The pioneer work of

Manson and the concepts based on it mark the real beginning of the scientific study of insect transmission of disease

In 1893, Smith and Kilbourne published their classic work on the transmission of the Texas fever of cattle by the cattle tick This very thorough investigation of the transmission of an animal disease by a small arthropod also established new concepts and stimulated further studies in the field of medical entomology

Bruce, in 1895, demonstrated the association of the tsetse fly and the nagana disease of cattle in Africa, this was soon followed by the work of Ross (1898) and others proving that mosquitoes were responsible for the transmission of malaria These epoch-making discoveries led to the proof in 1900 by the United States Army Yellow Fever Commission that yellow fever is transmitted by mosquitoes and is dependent upon these insects for its existence   (For a more complete summary of insect transmission of animal diseases, see Chap XVI)

Further advances in the field of plant pathology were made in 1909 and 1910 when Petri showed that the olive fly (*Dacus oleae*) could transmit the olive-knot disease   The intricate symbiotic association of this insect and several species of bacteria, including the olive-knot pathogen, illustrates a high degree of adaptation between insects and bacteria that is of great significance in plant pathology

In 1911, E F Smith reported proof of the transmission of bacterial wilt of cucurbits by the striped cucumber beetles This was followed by more complete reports by Rand (1915) and by Rand *et al* (1916, 1920) who proved conclusively that the cucumber beetles were vectors of the disease and probably the only means of transmission of the disease in nature   They showed also that the pathogenic bacteria were preserved over winter in the bodies of the insects and that the overwintered insects were responsible for primary infection in the spring The disease appears to be entirely dependent upon the insects for its spread and survival

In the same year, Norton (1911) published a paper of considerable historical interest. This was a short article entitled "The health of plants as related to insects " It apparently was the first article of a general nature ever published on the subject of insects in relation to plant diseases   Norton reviewed

briefly the association of insects and plant diseases known at that time and called attention to the importance of the subject and the need for further study. He classified the action of insects on plants according to the following categories

1. Direct injuries
   a. Physiological troubles following injury
   b. Diseases caused by the presence of insects or their products
2. Diseases indirectly caused by insects (by dissemination of the pathogens)

Two years later, Heald (1913) published a well-organized summary of the agencies and methods of dissemination of plant pathogenic fungi. Using this article as a starting point, Gardner (1918) published a somewhat more extensive treatment of "The mode of dissemination of fungous and bacterial diseases of plants." In both these papers, the growing recognition of the importance of insects in the dissemination of plant pathogens is obvious.

A discovery of fundamental interest was made by Ball in 1918 when he demonstrated that much of the so-called "tipburn" of potatoes was caused by the feeding activities of the potato leaf hopper (*Empoasca fabae* Harris). His discussion of this injury gave rise to a new concept in plant pathology and led to further investigation of the toxic effects of insect feeding punctures and the many obscure diseases that are associated with such injuries. Since then, numerous diseases of similar nature have been described, and much has been learned about these "toxicogenic" insects and the diseases that are caused by them.

In the 30 years following the pioneer work of Waite, a considerable amount of work on the subject of insect transmission of plant diseases appeared in the literature. These reports were widely scattered in periodicals and bulletins. In 1920, Rand and Pierce published an article entitled "A coordination of our knowledge of insect transmission in plant and animal diseases." In this 42-page article, "written primarily in the interests of plant pathologists," the authors summarized and coordinated the literature in both fields of work. They recognized and pointed out certain principles common to insect transmission of both animal and plant diseases and used these principles as a basis for classification of the known phenomena of insect transmission. As a direct result of the interest created

by this paper, the American Phytopathological Society and the American Association of Economic Entomologists at their annual meetings in Toronto, Canada, on Dec 31, 1921, held a joint symposium on "Insects as disseminators of plant diseases" (Rand, Ball, Caesar, and Gardner 1922)   This symposium created still greater interest in the subject and made evident the need for closer cooperation between plant pathologist and entomologist

In 1921, there appeared a book entitled "Tier and Pflanze in Intracellular Symbiose," written by Buchner, a German entomologist who for a number of years had been investigating the phenomena of symbiosis between insects and microorganisms In 1930, the book was revised and its scope expanded under the title "Tier and Pflanze in Symbiose"   These books bring together for the first time the scattered information on the fundamental phenomena of symbiosis between insects and microorganisms, although the subject is not treated from the viewpoint of plant pathology, the problems dealt with are very significant in the study of insects in relation to plant diseases

The increasing interest in the subject of insects in relation to plant disease was shown in 1929 when Boning published in Germany an extensive critical review of the literature on "Insekten als Uebertrager von Pflanzenkrankheiten"   The growing importance of virus diseases from this standpoint is manifested by the preponderance of citations of literature in this field In 1931 and 1933, Smith published summaries of the accumulated knowledge of virus diseases in which he devoted considerable space to the subject of insect transmission of viruses   These were followed by a general textbook of virus diseases of plants (Smith 1937)

The appearance of the destructive and spectacular Dutch elm disease in Europe and America and the proof of its dependence upon insects have, in a very dramatic way, focused the attentions of both entomologists and plant pathologist on the importance of insects as vectors of plant diseases   Investigations of this disease have demonstrated to a striking degree the necessity of cooperative effort in the study of insect-transmitted diseases

The general subject of insects in relation to plant diseases was reviewed in 1935 by Leach, who pointed out its importance and promise as a field of research and urged its further develop-

ment A growing interest in the subject was manifested in the symposium on insects in relation to plant diseases conducted jointly by the Entomological Society of America, the American Association of Economic Entomologists, and the American Phytopathological Society at Indianapolis, Ind , in 1937 In this symposium, various aspects of the subjects were treated by Granovsky (1938), De Long (1938), Kunkel (1938), Searls (1938), Leach (1938), Poos (1938), Ingram (1938), and Stevens (1938)

In general, the progress of plant pathology has paralleled that of human and animal pathology The importance of insects in human pathology has led to the development of the extensive and rapidly growing field of medical entomology The trend of events seems to indicate that a similar development is taking place in the science of plant pathology

HOW INSECTS AID IN THE SPREAD AND DEVELOPMENT OF PLANT DISEASES

Insects influence the development of plant diseases in many different ways For convenience the various types of association may be classified according to the particular function performed by the insect Insects may be responsible for, or aid in

1 Direct production of a disease without the help of a pathogen, usually by the injection of a toxic substance into the tissue of the plant

2 Dissemination of the pathogen

3 Inoculation of the suscept with the pathogen

4 Ingression of the pathogen into the suscept

5 Invasion of the suscept by the pathogen

6 Preservation of the pathogen

Direct Disease Production.—Some insects, in feeding upon plants, cause only mechanical destruction of the tissues upon which they feed Others cause injury to tissues some distance removed from the point of feeding The degree of injury may vary from relatively local lesions to a general systemic effect on all parts of the plant The exact mechanism of the injury is obscure in most cases, and there is need for much more study of this group of diseases In some cases, there is convincing evidence that a toxic substance is injected into the tissues of the plant In others, the physiological processes may be disturbed by local mechanical injury to vital tissues As examples of nonparasitic diseases caused by the feeding of insects may be

mentioned hopperburn of potatoes, mealy-bug wilt of pine-
apples, the green-spotting diseases of pineapples, and psyllid
yellows of potatoes   These and other similar diseases are dis-
cussed in more detail in Chap V

Dissemination of the Pathogen —Most plant pathogens, under
favorable conditions, produce relatively large quantities of inocu-
lum   But before reinfection can take place, the inoculum must
be dispersed to new plants or new infection courts   The spread
of plant diseases and the development of epiphytotics depend
to a great extent upon the efficiency with which the pathogen is
disseminated   Inoculum may be disseminated in many different
ways, wind, water, insects, man, and other animals being some
of the most important agents   The relative importance of the
different agents of dissemination varies greatly with different
diseases   It is obvious that an accurate evaluation of the
relative importance of the different methods is essential to an
intelligent control program

Wind is perhaps the most effective agent of dissemination of
many kinds of inoculum, but the inoculum of many plant patho-
gens is not well adapted for wind dispersal   Spores of patho-
genic fungi and cells of bacteria are often produced in sticky
exudates that become hard on drying, precluding almost entirely
the possibility of effective wind dispersal   In such cases, insects
are known to play an important role

The dissemination of pathogens is the most obvious way in
which insects are concerned in the development of plant diseases
For this reason, although other functions have been recognized,
the idea of dissemination has almost exclusively predominated
all published literature of a general nature on the subject   The
dissemination of the pathogen, however, is only one of several
critical stages in the development of a disease

Inoculation —To "disseminate" is to scatter, broadcast, or
diffuse   To "inoculate," as the term is used in plant pathology,
is to transport inoculum to a particular part of the plant where
infection may result   Wind is a common agent of dissemination,
but wind inoculation occurs only when, by chance, the inoculum
falls on the right place   Most of the inoculum disseminated by
wind never reaches the proper infection court and is consequently
wasted   Many insects, because of their habits of visiting certain
species of plants and specific organs of those plants, are not only

agents of dissemination but are also very effective agents of inoculation   They transport the inoculum to the most favorable place for infection with little loss of material   The honeybee and blossom blight of fruits, the sphinx moth and anther smut of pinks, the pollen-eating flies and ergot of cereals, and stigmatomycosis of various plants are well-known examples of this type of insect inoculation   More recently described associations of this nature are those involved in the so-called "fruit spoilage" of figs (Smith and Hansen 1931)   Endosepsis (Caldis 1927), souring (Caldis 1930), and smut (Hansen and Davey 1932) all depend upon certain fig insects for introduction of the respective pathogens into the interior of the young fig fruit where infection occurs   These associations are treated more fully in Chap VII

The systemic disease of red clover caused by *Botrytis anthophila* Bond , described by Bondarzew (1914) and Silow (1933), is especially illustrative   The spores of this pathogen are transported by the bees that pollinate red clover   The spores, along with pollen grains, are deposited by the bees on the stigmas of the clover flowers, where they germinate   The mycelium of the pathogen, along with the pollen tube, grows and penetrates the ovary   The fungus continues to grow slowly and persists under the seed coat but does not destroy the seed   Infected seeds, when planted, give rise to systematically infected plants   The fungus grows out into the young flowers, many of which are blighted, and the spores are formed over the surface of the anthers (see Fig 125)   Bees visiting the blighted blossoms become contaminated with spores and spread the infection to other plants, completing a cycle closely paralleling the process of insect pollination of flowers

Ingression —All our higher plants have an effective natural protection against pathogens in the form of cuticle or cork   The entrance or penetration through this external covering by the pathogen is necessary for infection   This process of gaining entrance has been termed "ingress" by Whetzel (1929)   Some pathogens are able to penetrate this protective layer by their own resources, but many depend upon wounds   The feeding or oviposition wounds of insects constitute one of the most important avenues of ingression for plant pathogens   The significance of insects as agents of dissemination and inoculation is greatly

enhanced when they serve also as agents of ingression   In some cases, this aid to ingression overshadows the importance of dissemination and inoculation   The role of the woolly aphid in the development of perennial canker of apple trees as described by Childs (1929) and McLarty (1933) is an excellent example of this type of relationship   These investigators have shown that *Gleosporium perennans* Zeller is strictly a wound parasite and that reinfection of a canker must take place each year   Although plenty of inoculum is present in the canker, reinfection does not occur in the absence of the aphid   This insect lives in the crevices of the canker and makes the wounds that are necessary for infection on each succeeding year's growth of callus   Thus the so-called "perennial" canker is actually annual, and the apparently perennial character depends entirely on reinfection each year through wounds made by the aphids which, although essential for the development of the disease, are of relatively little importance in dissemination of the spores

Another example is afforded by the relation of soil insects to crown-gall infection   Banfield (1931) and Ricker and Hildebrand (1934) have shown that white grubs and several other soil insects are common and effective agents in the opening of infection courts for crown gall, although they are probably of little significance in actual dissemination of the pathogen

Invasion —Insects may perform the functions of dissemination, inoculation, and ingression in various combinations   They also may aid the plant pathogen in the invasion of the plant tissues   Leach, Orr, and Christensen (1937) have reported a case in which the insect aids the pathogen in the process of invasion of the tissues but has no part in the processes of dissemination, inoculation, or ingression   Two wood-boring beetles [*Monochamus scutellatus* (Say) and *M notatus* (Drury)] commonly infest fallen logs of coniferous trees   By boring in a radial and tangential direction into the heartwood of pine logs, they greatly hasten the rate of invasion and decay of the heartwood by the wood-rotting fungus, *Peniophora gigantea* (see Figs 131 and 132) The fungus spreads rapidly in the sapwood but can invade the heartwood in a radial and tangential direction only very slowly With the aid of the insects the fungus accomplishes radial and tangential invasion, after which longitudinal invasion progresses rapidly   The fungus is disseminated and gains entrance inde-

pendently of the wood-boring insects but invades and decays the heartwood very slowly in the absence of the insects

Preservation of the Pathogen —In nearly all parts of the world, with the exception of some of the more humid tropical regions, there is some period of the year when it is difficult for plant pathogens to survive The difficulty of survival is usually caused indirectly by an absence of the necessary susceptible plants on which they can persist   In the more northern latitudes, the critical period is in the winter when the susceptible plants are killed or made dormant by low temperatures   In the warmer and more arid regions, the heat and drought may be the limiting factors   Successful pathogens are those which, by means of some special adaptations, are able to survive these unfavorable periods and cause infection when conditions are again favorable

Mere survival of the pathogen, however, is not sufficient The pathogen must survive under conditions that provide a suitable means of reinfection   Some pathogens, capable of saprophytic growth, remain dormant in the soil or plant refuse through the unfavorable period and, when plant growth is renewed, produce inoculum that is disseminated by wind or other agencies Some pathogens are adapted for survival in the roots or stems of perennial plants   Others survive in seed or other plant parts used for propagation   When a pathogen is largely or entirely dependent upon insect transmission, it is often adapted to survival within or on the body of the hibernating insect   As examples of some of the insects that are known to aid in the preservation of plant pathogens may be mentioned the corn flea beetles that harbor the bacteria causing bacterial wilt of corn, the pine bark beetles harboring the blue-stain fungi, the seed-corn maggot in the puparia of which the soft rot bacteria may survive, and the cucumber beetles which preserve *Erwinia tracheiphila* over winter

THE POSSIBLE ROLE OF INSECTS IN THE ORIGIN OF NEW DISEASES AND THE EXTENSION OF OLD ONES

One other aspect of the association of insects and plant diseases generally has been overlooked   This is the possible and probable role of insects in the sudden appearance of new and destructive plant diseases   We are accustomed to thinking of plant diseases largely in terms of the pathogen, an organism of ancient lineage

that has had in common with other plants a long and slow process of evolution during which its efficiency as a pathogen also has evolved   But a disease is not an organism   It is a biological process and is the result of the interaction of two or more organisms, influenced by a large number of environmental factors The organisms involved in the production of the disease may have evolved slowly, but the disease itself may have come into existence in a different manner   For the purpose of illustration, let us consider the Dutch elm disease, first recognized in south Holland in 1919 (Spierenburg 1922)   There seems to be considerable evidence that it has spread from this center to most of the countries of Southern and Western Europe and also into the United States (May 1931, 1934)   Its origin is obscure, but the general assumption seems to be that it may have been introduced into Western Europe from some other part of the world   The author has no original evidence with which to challenge this assumption but wishes to suggest a means by which the disease, in the sense of a biological process, may have originated in Western Europe within relatively recent years   The bark beetles, which constitute the principal agent of dissemination of *Ceratostomella ulmi*, were known in Europe and America for many years prior to the appearance of the Dutch elm disease (Collins 1935) At the present time, there are large areas in which the beetles occur but where the disease is absent (Felt 1934), but these areas appear to be rapidly diminishing as the result of the spread of the disease by contaminated beetles   This fact, although by no means constituting conclusive proof, would seem to indicate that the association is probably not one of long standing   *C ulmi* is a virulent pathogen on elms, but it grows well as a saprophyte on dead wood or bark, and variant strains are known to occur (Walter 1937)   The fungus can infect only through wounds, and its spores are not well adapted to wind dissemination   In the absence of a suitable insect vector, it would probably exist chiefly as a saprophyte on dead wood and perhaps be disseminated from one dead tree to another by insects inhabiting dead wood   As such it would attract no attention, and the injury caused would scarcely justify consideration as a disease   But when a virulent pathogenic strain of the fungus becomes associated with the Scolytid bark beetles, which, because of their habit of feeding on twigs of vigorous healthy trees, prove to be ideal

vectors, a very destructive disease is the result   Furthermore,
the elm bark beetles, which by their nature can breed only in
weakened or dying elm trees, find the association to their advan-
tage   By transporting the spores of *C ulmi* and introducing
them into feeding wounds, they cause infection of more trees,
provide themselves with an abundance of weakened or dying
elms, and thereby rapidly increase in number   More vectors,
more disease, more dead or weakened trees, and more
vectors!   A vicious circle resulting in an epiphytotic disease that
threatens to destroy one of our most valuable trees!   This order
of events in the origin of the Dutch elm disease is purely theoreti-
cal, but it is well within the realm of possibility and deserves
consideration   It is suggested here primarily to illustrate one
of the many significant aspects of the association of insects with
plant diseases

There is evidence that fungi of some sort are constantly
associated with most, if not all, Scolytid bark beetles   It would
be interesting to know what fungi, if any, are regularly associated
with the elm bark beetles in the regions where the Dutch elm
disease does not occur   The author has seen no record of this
having been determined

Many insects as well as plant pathogens are, or until recently
have been, relatively local in their distribution   With increased
commerce and travel throughout the world, they are becoming
more widespread in spite of all efforts to control them   With
promiscuous intermingling of insects and pathogens, it would
be surprising if new combinations and associations were not
formed in which an insect and a pathogen (neither of which alone
may be conspicuous or of economic importance) working together
may give rise to a destructive disease   This idea first presented
by Leach (1935), has been expressed independently by Carter
(1936)

The invasion of new areas by insects also may influence pro-
foundly the distribution of certain well-known destructive dis-
eases   Curly top of sugar beet, for example, occurs in North
America only in the arid regions of the western United States
According to Carter (1930), it is limited to these regions because
the insect vector (*Eutettix tenellus*) cannot thrive in the more
humid regions   It has been shown by Fawcett (1927) that a dis-
ease he identified as curly top in Argentina is spread by another

leaf hopper (*Agallia stictocollis*)   This insect is said to thrive in regions of relatively high humidity   If it should be introduced into the United States and prove to be a vector of curly top, there is a strong probability that the range of the disease would be greatly extended

THE CLASSIFICATION OF THE PHENOMENA OF INSECT TRANSMISSION OF DISEASES

At various times, several authors have drawn up systems of classification of the different kinds of insect transmission of diseases   Some of these have been more complete than others, yet none has been entirely satisfactory   Obviously, all have been based on incomplete knowledge of the various phenomena, and none has claimed any degree of finality   The chief aims of such classifications are to clarify one's thoughts and to provide a better perspective of the problem   With these purposes in mind and as a matter of historical interest, some of the more important classifications are given below

Rand and Pierce (1920) were the first to present a scheme of classification applicable to plant diseases   Their classification is as follows

1   External transmission of parasitic microorganisms
    a   External dissemination and direct inoculation by the insect vectors
    b   External dissemination and accidental infection without direct inoculation
2   Infection through insect wounds without dissemination by the wounding agent
3   Internal transmission of parasitic microorganism
    a   Mechanical internal transmission
    b   Biological internal transmission

Karl Boning (1929) criticized the classification of Rand and Pierce on the basis that the primary criterion of internal and external transmission was an artificial one and involved too much overlapping   He proposed the following simplified scheme of classification

1   Dissemination without wounding
2   Dissemination with wounding
    a   Insect obligatory
    b   Insect not obligatory

A classification of the roles played by insects in the spread and development of plant diseases was devised by the author and has been used for several years in teaching a class in "Insects in relation to plant diseases" This classification is as follows

I Wounding of the plant by an insect without dissemination of a pathogen
     A Insect toxicogenic (psyllid yellows, mealy-bug wilt of pineapple, etc)
     B Insect not toxicogenic (white grubs and crown gall)
II Dissemination of a pathogen by an insect without wounding the plant
     A Mechanical dissemination only (sphinx moths and anther smut, flies and ergot)
     B Biological dissemination (rare)
         1 Insect not obligatory (flies and fire blight)
         2 Insect obligatory (theoretically possible but no examples known)
III Dissemination of a pathogen by an insect with wounding of the plant
     A Mechanical dissemination only (bark beetles and blue stain, elm bark beetles and Dutch elm disease)
     B Biological dissemination
         1 Insect not obligatory (dipterous insects and bacterial soft rot, *Dacus oleae* and olive knot)
         2 Insect obligatory (cucumber beetles and bacterial wilt of cucurbits, apple maggot and bacterial rot of apples)

Similar classifications have been made by several workers interested primarily in animal diseases The phenomena found in insect transmission of animal diseases offer different criteria, and as a result the systems of classification are somewhat different A few of these are given below for the purpose of comparison

Riley and Johannsen (1932) group the ways in which arthropods may affect the health of man and other animals in the following manner

1 Directly poisonous
2 Parasitic, living more or less permanently on the body of their host and deriving nourishment from it
3 Transmitters and disseminators of disease, functioning as
     a Simple carriers
     b Direct inoculators
     c Essential hosts of pathogenic organisms

Folsom and Wardle (1934) recognize the following types of association between insects and diseases of man and animal.

1 Toxic inoculation
    a Venomous biters
    b Venomous stingers
    c Irritant caterpillars
2 Entomiasis (disease caused by actual presence of an insect in the host body)
3 Mechanical transmission
4 Cyclical transmission (insect an essential alternate host for a part of the life cycle of the microorganisms)

Huff in 1931 published "A proposed classification of disease transmission by arthropods" The essence of this classification is given below

1 Biological
    a Cyclopropagative (organisms undergo cyclical change and multiply within the vector)
    b Cyclodevelopmental (organisms undergo cyclical change but do not multiply within the vector)
    c Propagative (the organisms undergo no cyclical change but multiply within the vector)
2 Mechanical (organism undergoes neither cyclical change nor multiplication within the vector)

Certain factors must be kept in mind in comparing these different schemes of classification   The term "biological" has been used with many different connotations   Strictly speaking, any kind of insect transmission is biological, for living agents are involved   The term is generally used in a restricted sense in contrast with the term "mechanical," but here too its use has not been consistent   Biological transmission, as used in plant pathology, generally implies that the pathogen lives and multiplies in the body of the vector   When used in reference to virus diseases it has a slightly different connotation   In plant pathology, biological transmission is not synonymous with cyclical transmission   Cyclical transmission occurs only when the vector serves as an essential alternate host for the sexual stage of the life cycle of the pathogen   No such relationship is known in plant pathology, with the possible exception of *Phytomonas davidi* which parasitizes species of *Euphorbia* and is transmitted by *Stenocephalus agilis* Scop   According to Franca (1920), this protozoan undergoes a simple form of cyclic change in the body of its insect vector   Large forms are found commonly in the intestine, but smaller individuals appear, presumably after

a sexual process, and these invade the salivary glands and are introduced into the plant in the feeding process

THE BIOLOGIC AND EVOLUTIONARY SIGNIFICANCE OF THE ASSOCIATION OF INSECTS AND PLANT PATHOGENS

Research workers in phytopathology have, as a rule, considered insects merely as one of several agents that disseminate inoculum, to be disposed of in the ordinary routine study of a disease   It is the opinion of the author that the relation of insects to plant diseases is too important and too complex to be handled in such a summary manner   The association of insects with plant pathogens is, for the most part, not a mere matter of chance but rather a highly organized relationship which, in many cases, may have arisen out of a close association of insects and microorganisms over a period of 50 million years or more   It is a definite biologic phenomenon of evolutionary significance and has broad biologic and economic implications   As such it deserves more than routine attention   It merits the same type of sustained and coordinated thought and effort that has been given to other phytopathological problems of fundamental nature

As a biologic phenomenon the association of insects and plant pathogens is in many respects similar to that of entomophily, *i e ,* insect pollination   All students of botany or entomology are familiar with the remarkable evolutionary adaptations of insects and flowers   It will not be necessary here to describe the various details of these adaptations   Along with the morphological adaptations on the part of both insects and flowers, there has been built up a constant and regular association of insects and plants that is mutually beneficial to both parties of the association   Let us consider how this association came about   It is agreed by most, if not all, students of plants that our most primitive flowering land plants were wind-pollinated   Pollination was a matter of chance, and only a very few pollen grains reached the proper stigmatic surface   This necessitated the production of enormous quantities of pollen and obviously resulted in a tremendous waste of materials   But in one fortunate period long ago, insects discovered the food value of pollen and perhaps the associated secretion of nectar and began to make regular visits to those plants producing it   In this way, the pollen was transported with very little loss to the stigmatic surface of the proper

plant   This association had a survival value for both insects
and flowering plants and consequently has persisted throughout
the ages, developing to a state of very high efficiency   A little
reflection will show that the principle underlying this association
is essentially the same as that underlying insect dissemination
of plant pathogens   Some pathogens are disseminated only by
wind, in which case large quantities of inoculum are produced
but a relatively small part of it reaches an infection court and

FIG 42 —A sexual fruiting body of *Coprinus lagopus*   Basidiospores of two
sexes are produced on the gills of the mushroom   The mycelium arising from
a single basidiospore cannot produce another mushroom until it has been fertil-
ized by fusion with a mycelium of the opposite sex   (*Photograph by Dr W F
Hanna*)

survives   Other pathogens have become associated with insects
which transport them or their spores to the required infection
court   This is accomplished with a minimum of waste and a
maximum of efficiency, especially when the insects provide also
a means of ingress and of protection of the pathogen against the
elements   This type of association, like insect pollination, has a
survival value and numerous cases have persisted with remark-
ably complex adaptations on the part of both insect and patho-
gen   Survival value does not predicate benefits by both insect
and pathogen, but there are numerous cases of striking mutual
benefit and interdependence   As examples may be mentioned
the association between the blue stain of fungi and bark beetles

or that between the bacteria causing soft rot and the seed-corn maggot

It would not be logical, however, to drop the comparison here, for there are other important factors that have influenced the complicated adaptations associated with entomophily   With the development of insect pollination, the nature of the process led to an increase in cross-pollination in comparison with self-pollination   Cross-pollination increased the frequency of hybridization, and this in turn stimulated variation, a primary factor in evolution   Thus, insect pollination, by stimulating hybridization and variation, has speeded up the development of entomoph-
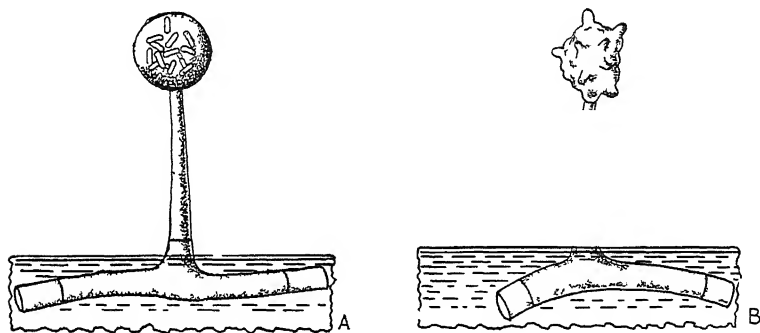
FIG 43 —Conidiophores of *Coprinus lagopus*   Note that the spores are borne in drops of a sticky solution   *A*, sporophore in a moist atmosphere *B*, the same after exposure to dry air   (*After Brodie*)

ily itself   This factor, so important in evolution, is apparently lacking in many of the associations of insects and plant pathogens and may account for the fact that the latter association is less obvious than entomophily

But recent investigations have shown us that the factor of hybridization cannot be removed entirely from the picture   With the discovery of heterothallism in fungi by Blakeslee (1904) and its further elucidation by Kniep (1928), Buller (1931), Stakman *et al* (1930), and others, the significance of hybridization in the evolution of fungi is more clearly discernible

Brodie (1931) has shown that flies are agents of "diploidization" in the fungus *Coprinus lagopus*, a process fundamentally analogous to insect pollination of higher plants   *Coprinus lagopus*, a mushroom commonly found on horse dung (Fig 42), is a heterothallic fungus   Each basidiospore formed on the

"inky-cap" mushroom, upon germination, forms a homosexual mycelium that is unable to reproduce the mushroom stage until it has been fertilized or diploidized by fusion with a mycelium of the opposite or complementary sex   Each of these homosexual mycelia produces conidia in drops of a sticky solution that prevents them from being blown around by air currents but that is attractive to flies (Fig 43)   Flies, by feeding on these droplets, transport the conidia from one mycelium to another (Fig 44)   The conidia promptly germinate and fuse with mycelia of opposite sex, diploidization results, followed by the formation of the mushroom stage   The spores may pass uninjured through the

Fig 44 —A diagram illustrating role of flies in the diploidization of the mycelium of *Coprinus lagopus*   Portions of two colonies of the fungus growing on agar are shown   Each colony originated from a single basidiospore, one of one sex (+) and one of the opposite sex (−)   Both mycelia are producing conidia in the usual drops of liquid   The fly in feeding has moved from one colony to the other taking with it spores that will germinate and fuse with the mycelium of the opposite sex, resulting in diploidization (fertilization)   (*After Brodie*)

digestive system of the flies, and drops of excrement usually contain spores of both sexes   Dowding (1931) has pointed out a comparable association between *Ascobolus stercorarius* (Bull) Schrot and mites and flies

A similar condition in the rust fungi has been revealed by the work of Craigie (1931) on *Puccinia helianthi* Schw and *P graminis* Pers   The rusts are heterothallic fungi   Reduction division occurs in the germinating teliospore (Fig 45), and on germination and infection the sporidia give rise to haploid mycelia   Pycnia (Figs 46 and 47) are produced on the haploid mycelium, but aeciospores, being dicaryotic, are formed only after diploidization   The process of diploidization has been described by Craigie (1931), Buller (1938), and others   It involves the transfer of

pycniospores from one pycnium to another of the opposite sex
Here the pycniospores germinate and fuse with a receptive
mycelium through the "flexuous hyphae" first described by
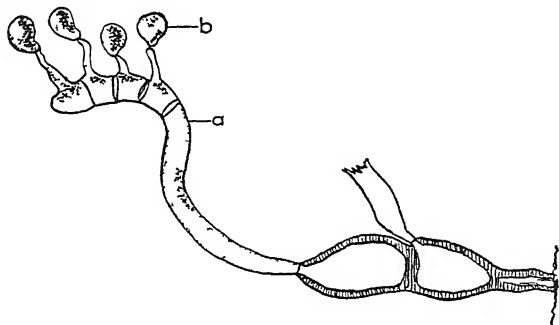
Fig 45 —A germinating teliospore of *Puccinia graminus* The complete
promycelium (*a*) of only one cell is shown Reduction division takes place in
the promycelium, and each sporidium (*b*) is in the haploid condition

Craigie (1933) (Figs 48 and 49) The transfer of the pycnio-
spores is often accomplished through the agency of insects The
pycniospores are exuded from the pycnium in drops of a fragrant,
sugary solution that makes them poorly adapted for dissemina-
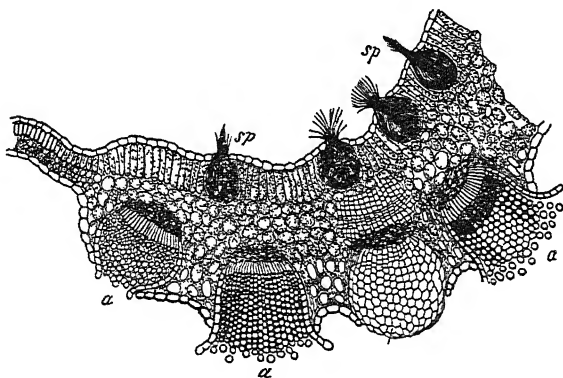
Fig 46 —A section through a barberry leaf infected with *Puccinia graminus*
showing the pycnia (*sp*) and aecia (*a*) The aecia do not develop until the
mycelium has been diploidized by the fusion of a pycniospore with a flexuous
hypha as shown in Fig 48 (*Modified, after Sachs*)

tion by wind but well adapted to insect transfer (Fig 50) Many
species of rusts have developed special characters that attract
insects and ensure the necessary interchange of sporidia Among
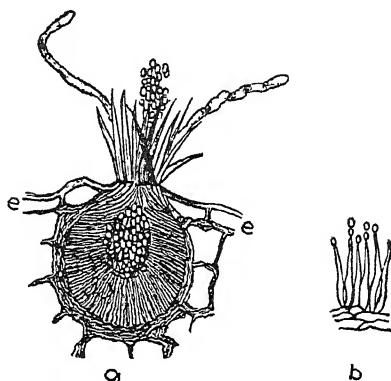
Fig 47 —A diagrammatic sketch of a section through a pycnium of *Puccinia graminis*   *a*, pycniospores oozing from the mouth of the pycnium surrounded by the spinelike setae and two of the flexuous hyphae, *b*, an enlarged view of a section of the pycnium wall showing how the pycniospores are borne *e*, epidermis of the barberry leaf   The pycniospores are functional gametes, and diploidization is effected when a pycniospore is transported to a pycnium of the opposite sex where it germinates and fuses with a flexuous hypha as shown in Fig 48   The sugary exudate is not shown in this sketch   (*Modified after De Bary*)

Fig 48 —The fusion of a germinated pycniospore with a flexuous hypha of a pycnium of *Puccinia helianthi*   The nucleus of the pycniospore has passed into the flexuous hypha   By repeated division and subsequent migration of the daughter nucleus into the adjacent cell, the mycelium of the pustule is rapidly diploidized   Aecium formation soon follows   Approx   1,500 ×   (*After Craigie*

these special adaptations may be mentioned the sugary solution
in which the pycniospores and flexuous hyphae are produced, the
bright orange color of the pycnia, and the distinct fragrance
of the sugary exudate

Flies, attracted by the drops of fragrant, sugary solution
formed on the bright orange-colored pycnia, effectively transport
the pycniospores from one pycnium to the other   Thus, insect
transportation of pycniospores results in diploidization and
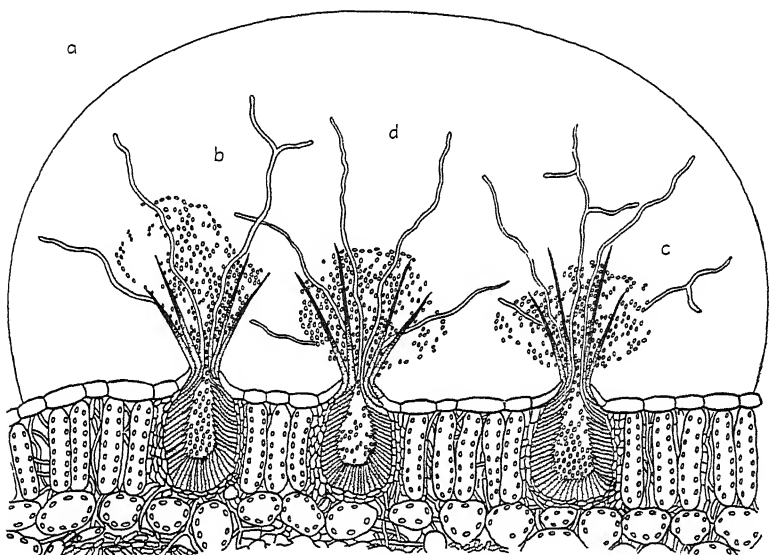
Fig 49 —A diagrammatic representation of pycnia of *Puccinia graminis*
showing the flexuous hyphae with which pycniospores of the opposite sex fuse
The curved line (a) represents the surface of the drop of sugary exudate, b
pycniospores, c, setae d flexuous hyphae   (*After Buller*)

increases the chances of hybridization and variation   The
relationship is quite comparable to insect pollination of flowering
plants   The large number of physiologic forms that occur in
this pathogen can be explained to some extent by the hybridiza-
tion that occurs on the barberry (Stakman *et al* 1930)   It is
probably not a mere coincidence that such a specialized adapta-
tion for insect "pollination" of a fungus, with resulting hybridiza-
tion, should be found in one of the most highly developed plant
pathogens and one in which physiological specialization has
reached such a high state of development

The association of insects with the pycnia of rust fungi was observed and discussed at length by Plowright as early as 1889, over forty years before the function of the pycnia was discovered Plowright observed 135 species of insects, including 31 Coleoptera, 32 Hymenoptera, 64 Diptera, and 8 Hemiptera feeding on the nectar He recognized specific adaptations of the rusts for insect attraction, listing the following six (1) the constant pro-
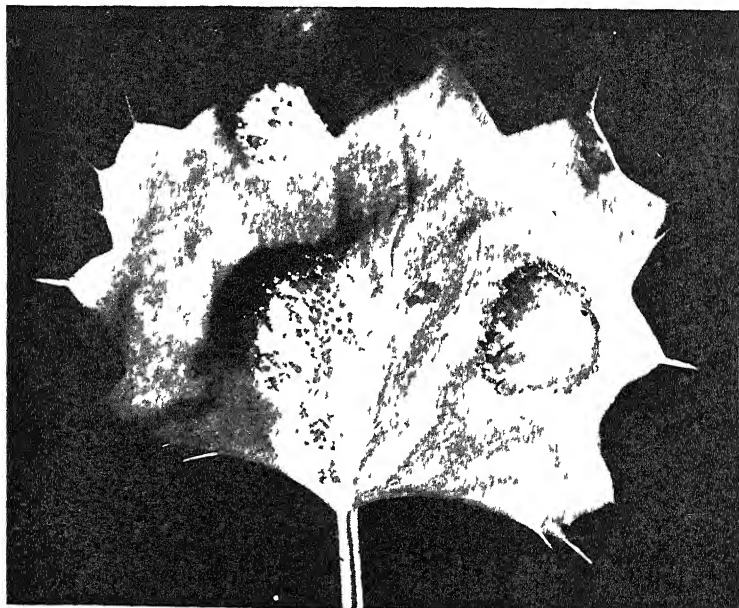
Fig 50 —A leaf of the common barberry infected with *Puccinia graminis*, showing four groups of pycnia with the droplets of sugary solution in which the pycniospores are borne   In natural color, the light areas are brilliant orange Notice the reflection of the light by each droplet   The sugary exudate has a faint but distinct fragrance   The entire fructification appears to be designed for the attraction of insects

duction of a sugary exudate in which the pycniospores are borne, (2) a definite fragrance that is associated with the pycnia of many species of rusts, (3) the bright orange color of the pycnia, (4) the abnormally erect position of affected leaves of some plant species, (5) the lighter color of pycnia-bearing leaves as compared with normal leaves of some plants, and (6) the dark spots contrasting with a lighter background characteristic of the pycnia of some rust species   This remarkable adaptation for the attraction of

insects is strikingly similar to the adaptations of flowering plants for the same purpose It is very probable that diploidization in the rusts, through the agency of insect "pollination," has had a directing influence in the evolution of this interesting and economically important group of fungi

The extent to which insects are involved in the mechanics of diploidization in other fungi is a problem for future study, because it has not yet received much attention It is of interest to note that Drayton (1934), who has described the sexual mechanism of *Sclerotinia gladioli* (Massey) Drayton, is of the opinion that insects may play a part in the sexual reproduction of that fungus He points out that the microconidia are borne in a mucilaginous matrix, the sticky nature of which would "allow the sporodochia to adhere to the bodies of soil-inhabiting animals or insects, and so be carried through the soil, possibly to receptive bodies of a compatible thallus "

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CHAPTER V

PLANT DISEASES CAUSED BY TOXICOGENIC INSECTS

It has become well recognized in recent years that a number of very destructive diseases of plants are caused by toxic substances introduced into the tissues of the plants by sucking insects These diseases often bring about greater destruction than do the more direct injuries caused by chewing insects Because of the indirect nature of the injury, the causal relationship of the insect frequently has been overlooked, and the true nature of the disease has escaped discovery Relatively little work has been done on diseases of this type, and the nature of the toxic substances and the methods of their action are poorly understood It is sometimes difficult to distinguish between pathological conditions resulting from purely mechanical injuries that may disturb the physiology of the plant and those resulting from definite toxic substances For example, the well-known hopperburn of potato and other plants is thought by some to be caused by a diffusible toxic substance introduced by the hopper, while others maintain that the mechanical injury caused by feeding is sufficient to account for the ill effects These differences of opinion will continue until we know more about the physiology of the diseased plants and of the insects involved in producing the diseases

Carter (1936a) has introduced two new terms to describe insects that may cause diseases by the injection of toxic substances He observes that, although the diseases caused by the insects may differ widely, they all have certain characteristics in common All are characterized by specific toxic effects, and the capacity to produce these is inherent in the insects concerned Species of insects producing the toxic substances were termed "toxicogenic" Since, as was shown by Carter (1936b), certain individuals of a species may, under some conditions, lose the ability to secrete the toxic substance, it was desirable to have a term to express the active toxic stage of a toxicogenic insect For this he proposed the term "toxiniferous"

A species capable of secreting a phytotoxic substance is called a "toxicogenic" species A toxicogenic insect is "toxiniferous" only in those stages of development when it can secrete the toxic materials In a later paper, the same author (1939) presented a general review of plant injuries caused by insect toxins in which he refers to this group of diseases as "toxemias," "phytotoxemias," or "toxicoses " Whatever term may be used to designate these plant injuries, they constitute a group of economically important diseases that are very imperfectly known

Diseases caused by toxicogenic insects may resemble virus diseases and are sometimes confused with them The systemic phytotoxic effects found in such diseases as psyllid yellows of potatoes and mealy-bug wilt of pineapples resemble virus diseases in many respects It is difficult without extensive experiments to determine to which category a disease belongs, and as a result the diseases are often confused in the mind of the student Carter (1936c) recognized this situation and has pointed out some of the more significant differences between the two classes of disease The essential differences are based largely on the inability of the toxic secretion of the toxicogenic insect to reproduce itself in the plant tissues The following table of comparison is based on that constructed by Carter but has been slightly modified and is given in a more generalized form

Diseases Caused by Toxicogenic Insects	Virus Diseases
1 Caused by a phytotoxic secretion of an insect	1 Caused by a virus
2 Toxic secretion is nonreproductive in plant	2 Virus is reproductive in plant
3 Recovery common	3 Recovery rare
4 Degree of injury related to the length of time, and number of insects feeding	4 Injury not directly related to length of time and number of insects feeding
5 Capacity to produce inherent in insect	5 Capacity of insect to produce acquired only by feeding
6 Disease not perpetuated by vegetative propagation or transmitted by grafting	6 Disease can be perpetuated by vegetative propagation and transmitted by grafting
7 Control of disease in proportion to insect control	7 Control of disease usually not in proportion to insect control

If the viruses prove to be of the nature of autocatalytic proteins, as indicated by the work of Stanley (1935) and others on tobacco mosaic, the similarities between these two groups of diseases will be greater still   The demonstration by Fukushi (1933, 1935) that the virus of rice dwarf is congenitally transmitted through the eggs of the vector has nullified to some extent item 5   The matter of reproduction on the part of the disease-inciting substance appears to be the most significant of the recognized differences   Even this distinction may have its exceptions   Severin and Haasis (1934) have demonstrated the transmission of the California strain of aster yellows to potato by the leaf hopper [*Macrosteles divisus* (Uhl)], but they were unable to recover the virus from infected potato plants   Leaf hoppers did not become viruliferous after prolonged feeding upon infected potato plants or after feeding upon the cut surface of tubers from plants that had shown symptoms of yellows   If these negative results are confirmed, showing that a virus will cause distinct symptoms on a plant but that the virus cannot be recovered from the infected plant or its progeny, it will be still more difficult to place borderline cases in one category or the other   Furthermore, it will be necessary to reinvestigate some of the diseases that resemble virus diseases but that are now interpreted as toxemias   For the best understanding of the nature of the disease caused by toxicogenic insects, it will be advisable to consider in some detail a few of the better known examples

Stigmonose —A F Woods (1900) was one of the first to recognize a definite plant disease as being caused by the indirect effects of insect feeding   Woods investigated a leaf-spotting disease of carnations that previously had been diagnosed as a bacterial disease (Arthur and Bolley 1896) and demonstrated that aphids, and not bacteria, were the actual cause of the trouble   Woods concluded that "the insect injects some irritating substance of an acid or enzymic nature into the wound, that this substance causes the increase of oxidizing enzymes in the cells which it reaches, and that these enzymes interfere with the nutrition of the cell by destroying the chlorophyll and setting up other changes which finally result in death "   Woods applied the term "stigmonose" or puncture disease to this abnormality   The term has since been used to designate diseases on many plants that are charac-

terized by local lesions caused by insect punctures as, for example, those often found on apples resulting from the feeding activities of the rosy apple aphid.

Since most phytophagous insects puncture plants in the process of feeding, the number of species that cause local lesions is extremely large. The type of injury varies from scarcely observable flecks to prominent and very characteristic necrotic lesions. It would seem unnecessary to discuss many of them here. A more inclusive account of this group of insect injuries has been presented by Carter (1939)

Hopperburn of Potato and Other Plants—Hopperburn is of particular interest because its history illustrates the extent to which the real cause of a disease of this kind may be overlooked and misinterpreted. It illustrates also the difficulty in distinguishing between the effects of simple mechanical injury and those of a toxic substance. The belated discovery of the true cause of the disease served in no small measure to call to the attention of both pathologists and entomologists the possible significance of toxicogenic insects in the production of plant diseases

In 1895, L R Jones, working in Vermont, described a disease of potato characterized by necrosis of the tips and margins of the leaves and called it "tipburn." He distinguished it from the fungus diseases, early blight and late blight, and concluded that it was due to excessive transpiration under the influence of high temperature, low humidity, and bright sunlight. In the following year, Osborn (1896), working in Iowa, called attention to the leaf hopper (*Empoasca fabae* Harris) as a potato pest and briefly described the injury caused by it. The extent of this injury was not fully recognized by entomologists, and plant pathologists usually confused the injury with the physiological tipburn described by Jones. E D Ball (1918), working in Wisconsin, was the first to distinguish clearly between the two types of injury. He demonstrated the nature and extent of the leaf-hopper injury and applied the term "hopperburn" to it. Ball (1919*a*, 1919*b*) clearly differentiated the symptoms of hopperburn from those of tipburn, pointing out that in the latter the mesophyll tissues between the veins were the first to die as a result of excessive transpiration, while in hopperburn the veins were affected first, and the injury later spread to the mesophyll that

was served by the veins (Figs 51 and 52)   Ball also expressed
the opinion that the death of the tissues in hopperburn was due
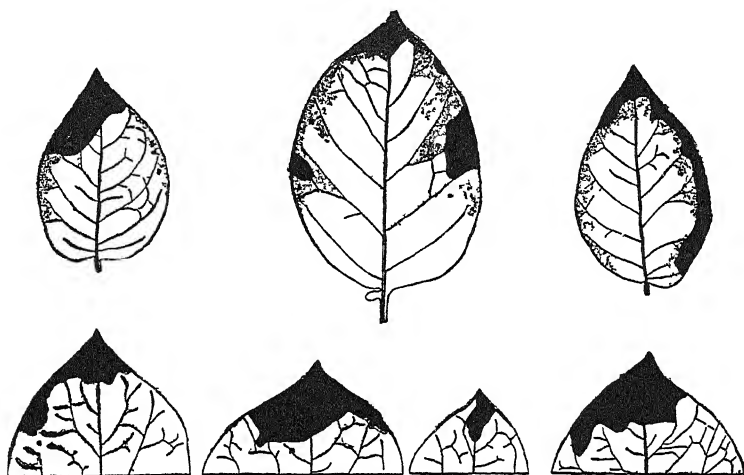
FIG 51 —Potato leaves affected with physiological tipburn   Note that the
necrotic or burned areas are not greatly influenced by the location of the veins
(*After Lutman*)
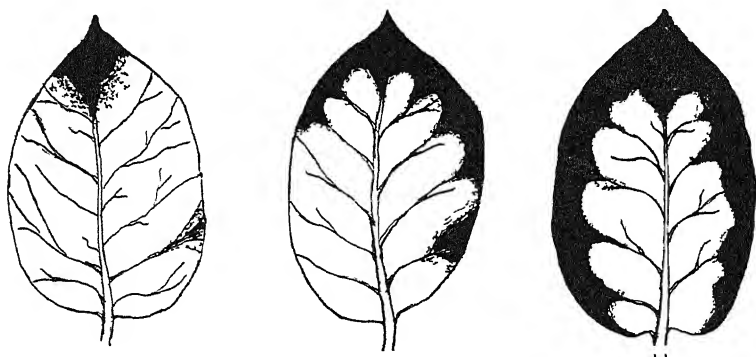
FIG 52 —Potato leaves affected with hopperburn   Diagrammatic sketch to
illustrate how the burning has its origin at a point on the vein where the hoppers
have fed   The necrotic areas tend to form a triangle with its apex at the feeding
point on the vein and its base at the leaf margin

to some specific toxic substance transmitted by the insect
Later Ball and Fenton (1920) suggested the substitution of "hop-
perburn" for "potato tipburn" because the name "covers
practically all that has formerly been designated as tipburn on

this plant " Lutman (1919, 1922), however, has shown clearly
that tipburn is a distinct disease and may be very destructive in
years when leaf hoppers are absent or in regions where they do not
occur   Furthermore, as pointed out in 1922 by Leach, the
necrosis of leaf tissue is only one stage of the injury caused by
the hoppers   When they feed on the young leaves, there is a
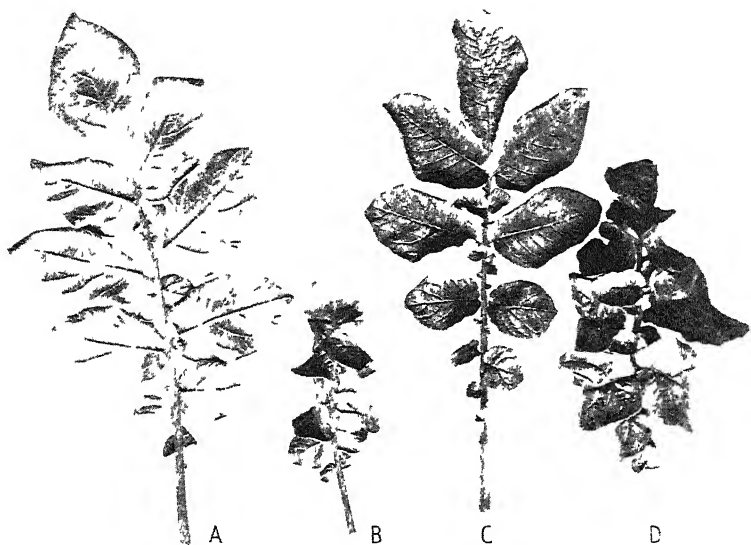pronounced retardation of development characterized by shorten-

FIG 53 —The leaf-curling effect of leaf-hopper feeding on potatoes   Leaves
B and *D* from plants infested with leaf hoppers in a cage   Note the curled leaves,
shortened internodes, and smaller size when compared with leaves from leaf-
hopper-free plants (*A* and *C*)   The leaves are of comparable age and from com-
parable locations on the plants   No necrosis or burning is present on either set of
leaves

ing of the petioles and crowding of the leaflets   There is also a
downward curling of the mid-veins accompanied by an upward
folding of the leaf along the mid-vein (Fig 53)   The tissues thus
affected are noticeably more brittle than normal ones   These
symptoms never result from excessive transpiration   It is
evident that there are two distinctly different diseases with
different causes, and they should not be confused

The potato leaf hopper (*E fabae* Harris) (Fig 54) is generally
distributed throughout North America and feeds upon a wide

variety of plants   It overwinters in the adult stage under leaves,
weeds, and other debris   The females become active in early
spring and feed on apple trees, beans, alfalfa, and a number of
weeds   The males do not come out of hibernation until later
During June, the females migrate to potatoes, beans, alfalfa, and
other host plants and are joined by overwintered males   Egg
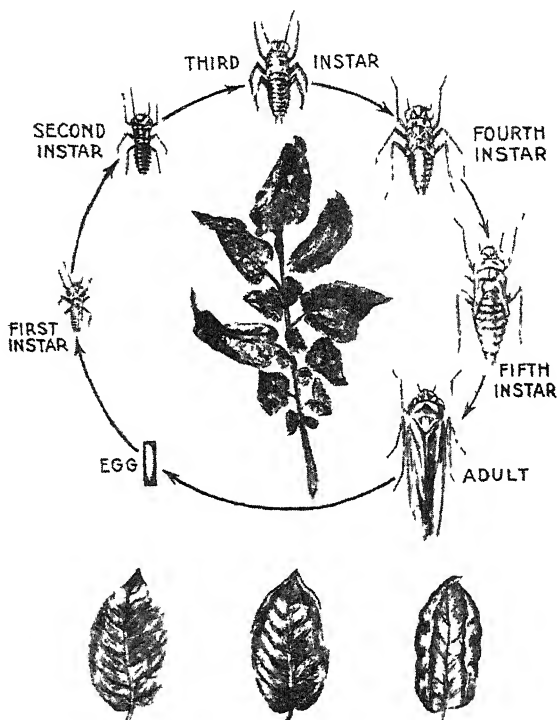
Fig 54 —The potato leaf hopper (*Empoasca fabae*) and potato leaves affected
with hopperburn   (*After Metcalf and Flint*)

laying begins soon, the eggs being inserted into the mid-rib and
leaf veins, chiefly on the undersurface   The eggs are only $\frac{1}{24}$
inch in length and are difficult to detect in the tissues   They
hatch after about 1 week, and the nymphs complete their develop-
ment, comprising five instars, in 2 to 4 weeks, depending upon
the temperature   The nymphs begin feeding immediately, and
the characteristic hopperburn soon appears   The nymphs are
wingless and unless disturbed complete their development on the

plant on which they are hatched   The winged adults are more active and migrate to other plants when those on which they are feeding mature   The various broods overlap extensively, and there are two to four broods each year

Following Ball's report on hopperburn of potato, similar injuries caused by the same insect on alfalfa, clover, apple, and other host plants were described by other workers who investigated more thoroughly the nature of the injury   The work of Eyer (1922), Fenton and Hartzell (1923), Jones and Granovsky (1927), Granovsky (1926, 1928, 1930), Monteith and Hollowell (1929), and Poos (1929) led to the conclusion that the direct cause of the injury was a diffusible toxic substance or enzyme injected into the plant by the leaf hopper   In 1930, Granovsky reported that microchemical tests revealed a greater accumulation of starch grains and sugars in affected tissues   There was also a clogging of vascular bundles and complete disorganization of the phloem region of severely injured tissue, phenomena held to be due to enzymic secretions by leaf hoppers in the course of feeding   Later investigations by Smith and Poos (1931), Smith (1933), and Johnson (1934) have verified the histological changes reported by Granovsky, but these authors consider it improbable that the leaf hopper injects a toxic substance   They suggest that the overaccumulation of carbohydrate products of photosynthesis above the point of feeding, as a result of the mechanical injury of the feeding punctures, is sufficient to cause the symptoms usually attributed to a diffusible toxic substance

Empoasca fabae, unlike a number of closely related but less injurious species, feeds almost exclusively on the vascular tissues, the mouth parts usually penetrating the phloem elements   The line of puncture becomes surrounded by a sheath of proteinlike substance shown by Smith and Poos (1931) to be largely of insect origin   The disorganization of cells some distance removed from the line of penetration would indicate that the secretions of the insect were to some extent toxic, at least locally   Johnson (1934) was unable to duplicate the disruption and plugging of the phloem tissues by repeated puncturing of a restricted region of leaf petioles with a fine glass needle   From this fact, it would seem highly improbable that the mechanical injury alone would so completely disorganize the phloem tissue   It would seem that a certain amount of a toxic substance must be injected by the

insect although the major symptoms and the ultimate death of
the tissues beyond the point of puncture may be the direct result
of the accumulation of photosynthetic materials brought about
by the clogging of the phloem   Toxicity is, at best, a poorly
defined concept, because the toxic substance may exert its effect
entirely through abnormal physiological reactions

There are other species of leaf hopper that feed upon the
vascular bundles but that do not cause injury as pronounced as
that caused by *E fabae*   The difference is probably due to an
unequal degree of toxicity of the saliva of the various species   It
is evident that neither a virus nor a widely diffusible toxic sub-
stance is involved in the production of hopperburn, for the disease
is not systemic, and the amount of injury is always in direct
proportion to the number of leaf hoppers present

The recognition of this disease and its relation to leaf-hopper
infestation has led to important discoveries in the principles of
insect and plant-disease control   While hopperburn was still
confused with tipburn caused by excessive transpiration, experi-
ments had shown that fairly effective control was obtained by
spraying the plants with Bordeaux mixture, although it was
known that Bordeaux mixture usually stimulated transpiration
This apparent paradox was explained by further experiments,
made after the role of the insects had been discovered, which
showed that the leaf hoppers were fairly well controlled by the
Bordeaux mixture   As the leaf hoppers are sucking insects and
Bordeaux mixture is not a strong contact insecticide, it was diffi-
cult to account for the control   It was concluded by Fluke
(1919), Kotila (1922), and others that the Bordeaux mixture
acted on the leaf hopper mainly as a repellent, discouraging
oviposition   De Long, Reid, and Dailey (1930a, 1930b), how-
ever, have shown that the leaves absorb enough copper from the
spray to be toxic to the leaf hoppers, especially the nymphs, as
they feed upon the cell contents   Although it has been known for
some time that copper from sprays was absorbed in small quan-
tities without injury to the cells, the effects of the absorbed copper
on sucking insects had never been extensively investigated   This
is essentially a new principle of insect control, and its possibilities
in the control of sucking insects have not been fully exploited

The influence of the degree of pubescence of certain varieties
and strains of clover and soy beans on hopperburn as demon-

strated by Hollowell, Monteith, and Flint (1927), Granovsky (1928), Pieters (1929), Jewett (1929), Poos and Smith (1931), and Johnson and Hollowell (1935) is of much interest   These workers show that the pubescent varieties are more resistant to leaf-hopper injury than the glabrous ones (Figs 55 and 56)   Pieters
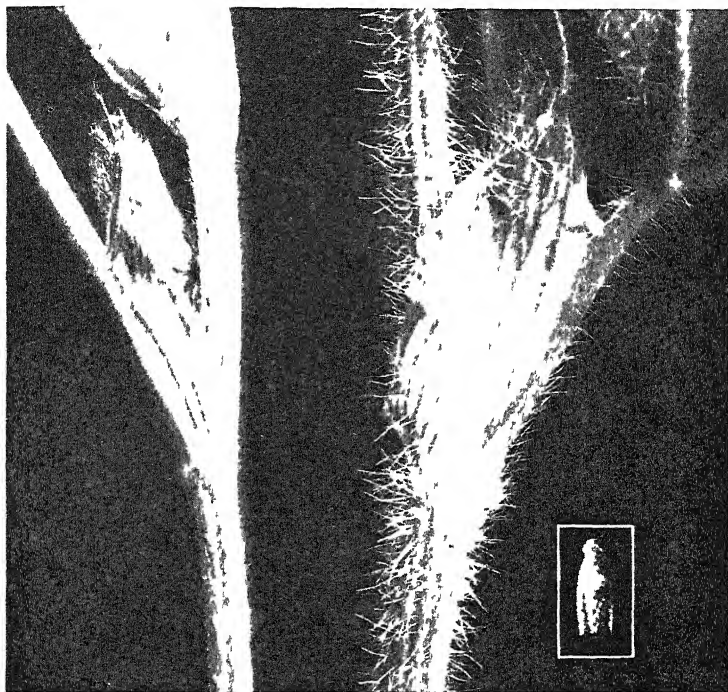

Fig 55 —Stems of two varieties of red clover and a mature leaf hopper showing the differences in pubescence and the relative size of the trichomes and the insect   Left, a stem from a very susceptible Italian red clover   Right, a stem of the relatively resistant Tennessee red clover   The resistance is attributed to dislike of the dense pubescence by the leaf hoppers   Insert a mature leaf hopper photographed on the same scale to show relative size of the insect and the trichomes   Approx 4×   (*After Monteith and Hollowell*)

has suggested that the predominance of the pubescent varieties of red clover in America can be explained by the unconscious selection of these types because of their resistance to the leaf hopper   The preference of the female hoppers for the glabrous tissue for oviposition is given as the factor responsible for the resistant, or escaping character although some workers believe other factors are involved

The resistance of certain varieties of apple trees to injury by the leaf hopper also has been explained on this basis by Schoene and Underhill (1937) who showed that the susceptibility to hopper-burn varied inversely with the amount of pubescence of the leaves of the different apple varieties   Varieties having foliage with scant pubescence (Albemarle Pippin, Bonum, and Early Harvest) were subject to serious injury while those varieties with densely pubescent foliage (Stayman Winesap, Winesap, and Delicious) were injured only slightly

Hopperburn, or yellow top, of alfalfa was long confused with the effects of fungus leaf spots, and little or no effort was made to

Fig 56 —The resistance of pubescent types of soy beans to hopperburn   The two large plants are highly pubescent and because of this fact have escaped the injury suffered by the remaining glabrous plants   (*After Johnson and Hollowell*)

control the leaf hoppers, but following the recognition of the part played by leaf hoppers (Jones and Granovsky 1927), the injury has been reduced considerably by delaying the early cuttings of alfalfa until just after the height of the egg-laying period   By delaying the cutting until most of the eggs are deposited, a high percentage of the eggs will be destroyed, and the later cuttings will be relatively free from hoppers (Graber and Sprague 1933, 1935, Searles 1934, and Jewett 1934)

Toxicogenic Capsid Bugs and Effects on Plant Tissues —Kenneth M Smith (1920) has studied the nature of the injury to apples caused by a toxicogenic "capsid" bug   Of five species of capsids that normally feed on the fruit and leaves of apple trees in England, only one species (*Plesicoris rugicollis*) is responsible

for appreciable damage This species causes the death of the tissues surrounding each feeding puncture, and when the insects feed on young apple fruits, the mature fruits become much distorted and severely russeted Smith showed definitely that the injury was caused by the secretion of a toxic substance in the saliva of the insect When the salivary glands of the different species were dissected out and placed on the cut surface of apple tissue, much of the tissue was killed around the glands of *P rugicollis*, while that adjacent to the glands taken from the remaining species was not injured Smith was unable to reproduce the injury by mechanical means Moreover, the fact that other species of capsid bugs, feeding in the same way on the same kinds of tissue, produced no such injury added weight to the evidence of the toxicogenic nature of *P rugicollis*

More recently, Leach and Smee (1933) and Leach (1935) have shown that a stem canker of tea and mangoes, an angular leaf spot, a fruit scab, and a fruit rot of mangoes are caused by the bug *Helopeltis bergrothi* Reut The various lesions produced by the feeding punctures of the insect simulate to a marked degree those caused by many pathogenic fungi and bacteria, and, according to Leach, the injuries have frequently been diagnosed as fungus diseases These authors were unable to find any microorganisms associated with the lesions and demonstrated the noninfectious nature of the trouble They conclude that the necrosis of the tissues is due to the injection by the insect of some irritant that diffuses through the cells from which the sap is sucked

Froghopper Blight of Sugar Cane —The Cercopid *Thomaspis saccharina* Dist causes a destructive disease of sugar cane known as "froghopper blight" Primary symptoms consist of pale chlorotic lesions at the point of puncture on a leaf The lesion gradually enlarges, assumes a pink color, and later becomes brown and necrotic There is a shortening of internodes resulting in a stunted plant Adventitious buds and roots are formed in excessive amounts near the base of the plants An increase in acidity of the cell sap is usually a characteristic of the affected plants Recovery may take place if growing conditions are favorable after the insects leave the plant

The disease has been studied extensively by Williams (1921) and Withycombe (1926) These workers conclude that the

disease is caused entirely by the feeding of the froghopper and not by fungi, bacteria, or viruses transmitted by the insect Injury results partly from the withdrawal of large quantities of moisture from the tissues and partly from the injurious effects of the salivary secretions of the insect The latter is accomplished in part by diastatic and oxidizing enzymes The rate of respiration is increased locally, and translocation is inhibited, resulting in a general upset in the metabolic equilibrium of the plant

The severity of the injury varies greatly with those factors of the environment which influence the general physiology of the plant Since the froghoppers oviposit in the soil, the soil reaction and soil type are considered to influence the prevalence of the insects

Mealy-bug Wilt of Pineapple —This disease has been known in Hawaii since 1910, but its cause has been known only since 1931 It has been reported also in Jamaica and in Central America (Carter 1934) It is extremely destructive and is considered the most important cause of pineapple failure in Hawaii Illingworth (1931) was the first to show that the disease was in some way associated with the attack of the mealy bug [*Pseudococcus brevipes* (Ckl)] Since 1931, it has been studied intensively by Carter (1932, 1933, 1935a, 1935b, 1936, 1937) and Carter and Schmidt (1935), who have added much to our knowledge of the nature of the disease They have shown that the mealy bug (*P brevipes*) is a toxicogenic insect and that the disease is caused by a toxic substance injected into the plant by the mealy bugs in the act of feeding

The symptoms of mealy-bug wilt are variable, being influenced by the size of the initial population of mealy bugs, the age and vigor of the plant, and other variable factors Carter (1933a) distinguishes two distinct types of wilt, quick wilt and slow wilt Quick wilt occurs primarily on young plants and usually follows the attack of an initial population of 50 or more mealy bugs (Fig 57) A short period of feeding is sufficient to produce the disease, but it requires about two months for the appearance of the typical symptoms Complete establishment of the colony of mealy bugs is not necessary for the production of quick wilt The leaves of affected plants become flaccid, droop, and turn pale, the color varying from very light dull green to pale yellow

or pink On older plants, some of the leaves take on a conspicuous red color The tips of the leaves become brown and dry The meristematic tissues are not killed, and cuttings made from affected plants grow normally Apparent recovery from quick wilt is common, but the fruits formed are small and of little commercial value

Slow wilt develops on older plants when a large colony of mealy bugs is built up from a small initial population Unlike quick wilt, slow wilt is always fatal The leaves wilt but,

FIG 57 —Mealy-bug wilt of pineapple "Quick wilt" This type most frequently occurs on young plants after the attack by a colony of 50 or more mealy bugs Plants often recover from quick wilt "Slow wilt" occurs on older plants after a colony of mealy bugs has been built up slowly from a small initial population Slow wilt is always fatal (*After Carter*)

because they are older, droop less than those affected with quick wilt The tip becomes necrotic, but the yellow and pink color characteristic of quick wilt is absent The roots collapse and are invaded by various secondary organisms that contribute to the final destruction of the plant Green spots associated with the feeding punctures of the mealy bugs are often found on plants affected with each type of wilt The wilt is usually more severe when the green spots are present, but Carter considers the production of green spots a distinct disease and not a symptom of mealy-bug wilt

The mealy bug (*P brevipes*) (Fig 58) is a member of the homopterous family Coccidae   In Hawaii, it is found on many kinds of plant, its principal hosts being pineapple, banana, sisal, and several species of grasses, including *Panicum barbinode* and *Tricholaena rosea* Nees   The insect is parthenogenetic and ovoviviparous, requiring about two months to complete its life cycle   The insects' bodies are covered with a characteristic

Fig 58 —A colony of pineapple mealy bugs (*Pseudococcus brevipes*) on a pineapple plant

white waxy secretion, and they also secrete honeydew   The mealy bugs are constantly attended by two species of ants [*Pheidole megacephala* (Fabr) and *Solenopsis geminata* Fabr var *rufa* Jerdon], and colonies will not develop normally when the ants are excluded

Based on the results of a long series of experiments, Carter's conclusions are that mealy-bug wilt is caused by a phytotoxic secretion that is diffusible but incapable of reproduction in the plant   The failure of quick-wilt symptoms to develop when colonies were built up slowly from a small initial population

was interpreted as the result of an antitoxic reaction on the part of the host. Evidence was presented to show that the toxicity of the secretions varied with the kind and condition of the host plants

Two hypotheses were considered in explaining the difference in toxicity of small and large initial populations. The first assumes that the mealy bugs from a single colony are equally toxic and that various quantities of toxic secretion are necessary, dependent on the general toxic level of the colony and the susceptibility of individual plants. The second assumes that the capacity to produce wilt is limited to certain individuals in the colony and that the development of wilt is governed by the incidence of toxic individuals. Because of the sedentary habit of the insect, it was considered unlikely that great variation in toxicity would occur among individuals of a single colony. A carefully planned field experiment in which a large number of plants were infested with mealy bugs, varying in number from 1 to 40 per plant, favored the first hypothesis and led Carter (1935) to conclude that "the most susceptible plant required a toxic dose greater than that provided by the feeding of one mealy bug," although in later experiments occasional plants wilted following infestation by single mealy bugs (Carter 1937). In general, the percentage of plants wilting increased with the number of mealy bugs, but the increase was not directly proportional. There appeared to be a point on the dosage scale that induced a disproportionate increase in wilt, dosages beyond this point resulting in only small increases in the number of wilted plants

Green Spotting of Pineapple and the Pineapple Mealy Bug — When Illingworth (1931) described the mealy-bug wilt of pineapple, he mentioned a characteristic green spot associated with the feeding punctures of the mealy bug [*Pseudococcus brevipes* (Ckl.)] and interpreted it as a symptom of wilt. Carter, however, in later investigations (1933b) showed that some of the mealy bugs did not cause green spotting even though they readily caused wilt. He concluded, therefore, that green spotting is a disease separate and distinct from pineapple wilt although both diseases are caused by the toxic secretions of the same insect

Mealy-bug colonies on the pineapple are found most commonly feeding on the white or light-green tissues at the base of the leaves

If the colonies are very large, they may extend up the leaf for some distance on the greener tissues   The green spots therefore are first seen on the white tissue as faint yellow-green homogeneous spots   As the leaf grows and becomes darker green, the spots maintain a darker color than the surrounding tissue   Often there is a concentric zone of light green around the darker center   Some of the spots may appear as raised welts, especially in older and partly shriveled tissues   Occasionally the center of
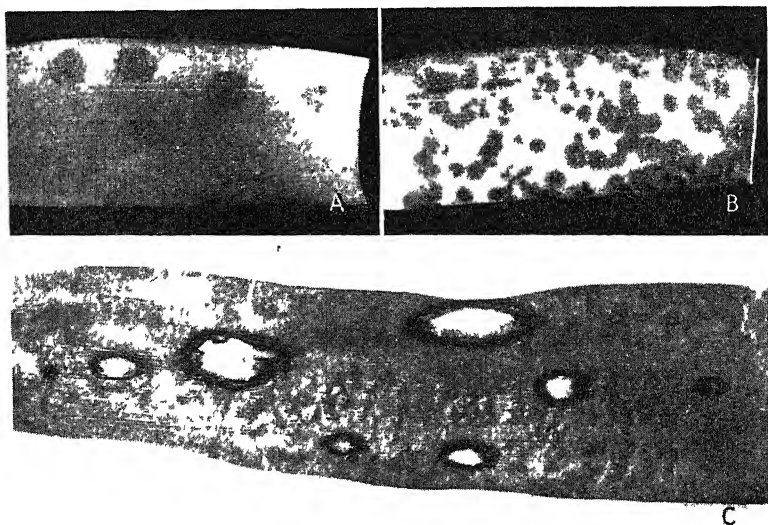

Fig 59 —Green spotting of pineapple   Photographs showing several of the various types of spot   *A* large green spots with dark centers, *B*, green spots in which color has persisted while surrounding tissue has become extremely chlorotic, *C*, a leaf with three distinct kinds of spot raised, weltlike spots in median area, nonelevated green spots near margin of leaf and several large spots of secondary necrosis   (*After Carter*)

the spots may become chlorotic and eventually necrotic   The spots vary in size from 1 to 10 millimeters in diameter, averaging 3 to 5 millimeters (Fig 59)

These spots are strikingly different from the feeding injuries made by a strain of mealy bugs that does not cause the green spots   These are usually visible as small, irregular-shaped, chlorotic spots with some rugosity of the leaf surface if the punctures are numerous   The spots usually are the result of a number of mealy bugs feeding for a prolonged period in one

place   Histological examination of the typical green spots reveals an increase in size and number of chloroplasts with no thickening of the cell walls   The protoplasm appears normal but contains flat polygonal bodies that stain heavily with Lugol's solution   Often the green tissues will appear as an island of green in chlorotic tissue   In the chlorotic spots formed by the feeding punctures of nongreen-spotting mealy bugs, the protoplasts are degenerate, and the cell walls are thickened   The area of injury is more localized and does not extend far beyond the actual area fed upon

It was observed that those mealy bugs which regularly cause the green spots are a darker gray color than the pinkish gray ones which do not cause the green spots   These darker individuals appear to move about more frequently as if the green spots make the tissue unsuitable for further feeding   Further examination of the insects showed that the dark-gray color of the green-spotting mealy bugs is caused by the presence of a dark-colored mycetome, the mycetomes of the "normal' mealy bugs being white   A microscopic study of the mycetome showed that it contains two different kinds of microsymbiotes   A yeast-like microsymbiote is always present in the mycetome of both types of mealy bug, and a bacterium-like, rod-shaped symbiote is found only in the dark-gray green-spotting mealy bugs   Further studies proved that the bacterium-like symbiote was pleomorphic and that by passing through a transitional stage it was transformed into a coccus form in the pink non-spotting mealy bugs (Fig 60)

It was further observed that mealy bugs taken directly from a grass host (*Panicum barbinode* Trin) contained the symbiote in the coccus form and failed to cause the green spots   In a series of feeding experiments, in which green-spotting mealy bugs were removed from pineapple and fed on Panicum grass for two or more generations and then returned to pineapple, the green-spotting capacity was lost   Parallel with this loss, the bacterium-like symbiote changed from the rod form to the coccus form   Continued cultivation on pineapple did not restore the green-spotting property of the mealy bugs or the rod form of the microsymbiote, indicating that the change was not reversible   From these and other experiment's Carter concludes that the green spotting is caused by a phytotoxic secretion of the mealy

bug that is conditioned by the presence of the microsymbiote in the rod-shaped form

Although the parallelism between the presence of the microsymbiote in the rod form is striking, it does not necessarily prove that there is a direct relationship between the two   There seems to be a possibility that the same factors that influence the toxicity of the insect's secretion also influence the mor-
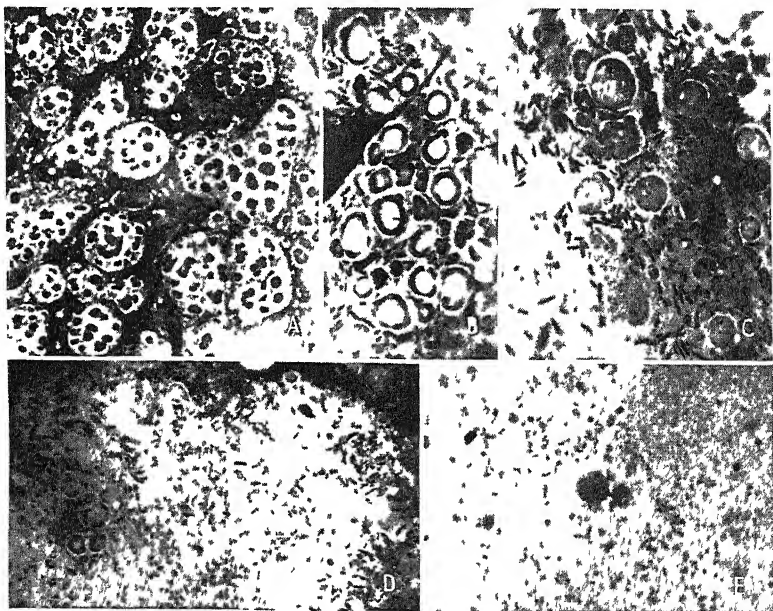

FIG 60 —Photomicrographs showing the microsymbiotes of *Pseudococcus brevipes*   *A*, mycetocytes containing the common form of symbiote, *B*, a preparation showing the rod-shaped form interspersed with vacuolated cells of the common form, *C*, rod-shaped symbiote from green-spotting mealy bug, *D*, intermediate forms of rod-shaped symbiote, *E*, coccus form of symbiote   (*After Carter*)

phology of the microsymbiote   This would not necessarily imply a causal relationship   The probability that the morphology of the microsymbiote conditioned the toxicity of the secretions would be greater if it were known that the microsymbiotes had any direct connection with the oral secretions of the insect   There is as yet no proof that this is true   The mycetome is found in close apposition to the mid-gut, but there is no direct connection   Neither has there been shown any connection of the mycetome with the salivary glands   Carter

(1936b) states, "The invariable presence of the rod-shaped form in green-spotting mealy bugs, the evidence of a transitional form, the complete absence of the rod, and the invariable presence of the coccus rod in nongreen-spotting mealy bugs are considered proof of the relationship between the symbiotes and the oral secretions of the insects" These facts may show strong indications of a relationship, but they could scarcely be considered as final proof of so complex a physiological relationship Further evidence will be necessary before the causal relationship of the pleomorphic changes in the microsymbiote and the toxicity of the secretions of the insect can be accepted as a proved fact

Ito (1938) has studied the life histories of the pink and the gray strain of this insect   It was found that the pink form reproduced parthenogenetically, producing only females, while the gray form reproduced sexually, producing both males and females This discovery may prove of some importance in future studies, although its significance is not obvious at present   In other aspects of their life histories, there was very little difference

Psyllid Yellows of the Potato   In 1928, a new and destructive disease of potatoes and tomatoes was reported by Richards from the western part of the United States   Richards and Blood (1933) have shown that the disease is definitely associated with the feeding processes of the nymphs of the tomato psyllid (*Paratrioza cockerelli* Sulc)   Unlike hopperburn and the russeting of apples by the capsid bugs, psyllid yellows is a systemic disease   Although the insects may feed on only a few of the leaves, the growth of the entire plant is affected to a striking degree

The symptoms vary somewhat with the number of insects on the plant and the length of the feeding period   The injury is greater when the insects are abundant, but the degree of injury is not always in proportion to the number of insects present   The feeding of 10 to 30 nymphs is necessary for the full expression of the disease   The intensity of the light also has a marked effect on the disease, the symptoms being more pronounced in bright sunlight

There is a marginal yellowing and an upward rolling of the basal parts of the leaflets (Fig 61)   The terminal leaves of the pigmented varieties assume a red or purple cast   In advanced stages, the older leaves become necrotic   The entire plant is

stunted by failure of the stems to elongate, the nodes swell, and the axillary buds may develop into aerial tubers or short shoots with swollen bases and small distorted leaves   Tuberization is suppressed in younger plants, and the stolons of older plants may develop secondary aerial shoots   The physiology

Fig 61 — A leaf from a potato plant affected with psyllid yellows showing the curling at the bases of the leaflets   (*After Richards and Blood*)

of the entire plant is affected strikingly, and the translocation of photosynthetic products is decidedly abnormal (Fig 62)

There has been some difference of opinion as to the nature of the disease   Binkley (1929) reported evidence which led him to conclude that the disease was caused by a virus transmitted by the psyllid nymphs, and Shapovalov (1929) observed what he thought was tuber transmission of the disease in potatoes

The most thorough and complete investigation of the disease to date is that of Richards and Blood (1933)   These authors were unable to demonstrate tuber transmission and could not prove the virus nature of the disease, although the possibility of its being caused by a virus was recognized   They showed that when the insects were removed from affected plants there was a cessation of the development of symptoms and a uniform tend-

FIG 62 —A potato plant affected with psyllid yellows   (*After Richards and Blood*)

ency to recover   The disease is produced only by the nymphs, the adults being nontoxiniferous   The ability to produce the disease is inherited by the insect without regard to its having fed on a diseased plant   Richards and Blood did not reach a final conclusion as to the nature of the disease, but the evidence presented strongly favors the view that the psyllid is a toxicogenic insect and that the disease is caused by a toxic substance injected into the plant by the nymph in the act of feeding

Smith (1937) has classified psyllid yellows as a virus disease caused by Solanum virus 18   This does not appear to be justified on the basis of the available evidence

Psyllids in general have well-developed mycetomes that harbor microsymbiotes (see Chap III)   In the light of Carter's work on the relation of microsymbiotes of mealy bugs to the green-spotting disease of pineapple, a study of the microsymbiotes of this insect seems desirable   Such a study of the tomato psyllid offers a good opportunity for testing the hypothesis that microsymbiotes are in some way concerned in the production of toxic substances secreted by the toxicogenic insects

Eyer and Crawford (1933) have studied the feeding habits of the tomato psyllid and the pathological histology of the disease The nymphs feed primarily on the leaves, usually on the lower surface, seeking out the vascular bundles   Their setae terminate most frequently in the phloem tissues or in the border parenchyma surrounding the phloem   There is no extensive injury or plugging of the xylem, although phloem cells are often killed A definite accumulation of starch is found in the parenchyma tissue, reflecting the inhibited translocation of photosynthetic materials   A more detailed study of the abnormal physiology of carbohydrate translocation has been reported by Eyer (1937)

The life history of the tomato psyllid has been described by Knowlton and Jones (1934) and by Daniels (1937)   The insect feeds on both wild and cultivated species of solanaceous plants It hibernates in the adult stage in warm, dry locations and in early spring feeds on clumps of wild perennial species of ground cherries (*Physalis lanciolata* Mich, *P longifolia* Nutt, and *Quincula lobata* Raf)   One or two generations may be spent on these weeds before migration to the potato fields begins   The small, spindle-shaped eggs are deposited most abundantly on young apical leaves on either the lower or the upper surface and are attached and supported by a short stipe (Fig 63)   From 5 to 150 eggs per day are deposited by a single female during an oviposition period varying from a few days to several months The insects are favored by warm, dry weather, and in favorable seasons there may be 8 to 10 generations   The eggs hatch in about five or six days and the nymphs crawl down the stipe and begin feeding on the plant tissues, passing through five instars About 15 days are required for the completion of nymphal

development There is usually a high mortality of nymphs at the first ecdysis The adults are winged and are quite active when the plants are disturbed

List (1939) has reported on the relation of temperature to the development of the psyllid and to its prevalence He concludes that it thrives best at about 80 degrees and is retarded in its development at higher temperatures A temperature of 95 degrees for only 2 or 3 hours per day permits little, if any, increase in numbers Its prevalence was correlated with
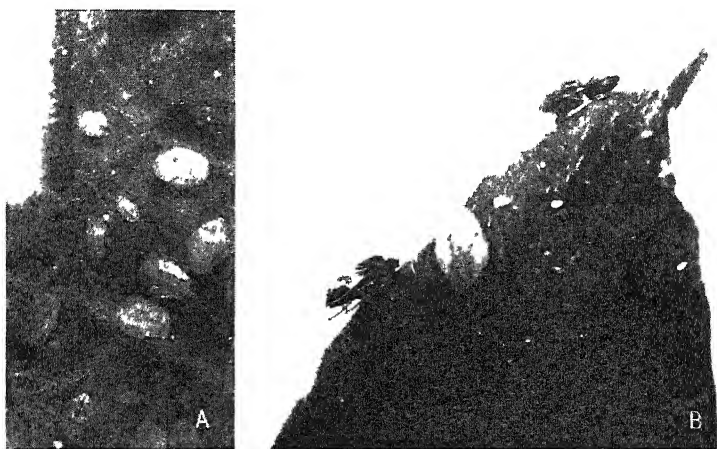

Fig 63 —The tomato psyllid *A* section of a leaf enlarged to show eggs and nymphs (approx 10 ×), *B*, two adults, a young and old nymph, and several eggs on a potato leaf (approx 12 ×) (*Courtesy of Montana Agricultural Experiment Station*)

temperatures in extensive field observations of a period of more than twenty years

The relation of temperature to migration and hibernation of the psyllid is discussed by List, who expresses the opinion that the psyllid hibernates in some breeding ground distant from the region of high summer infestations It is thought possible that with the coming of hot weather in the southern breeding areas the psyllids migrate and are brought into the farming regions by the same air currents that bring in the beet leaf hoppers This hypothesis is supported by the observations of Romney (1939), who has reported that the psyllids breed abundantly in early spring on *Lycium andersonii* Gray and *L macrodon* Gray

in the semidesert areas of southern Arizona   By the middle of
June, they have all migrated and are not to be found again until
an influx occurs in late October or early November   There is
obvious need for more extensive studies of the breeding and
migration habits of this insect in relation to the prevalence of
psyllid yellows

Successful control of psyllid yellows has followed the control
of the insects by spraying with lime-sulfur (List 1934, Daniels
1934, 1937)   Liquid lime-sulfur spray (1 gallon, 32 degrees
Baumé, to 40 gallons of water) applied with a power sprayer at
200 to 300 pounds pressure is recommended   Two applications
early in the growing season are required

Anasa Wilt of Cucurbits —A wilt of squash, pumpkin, and
other cucurbits caused by the squash bug (*Anasa tristis* De G)
was described in 1931 by Robinson and Richards   It was said
to be responsible for the complete abandonment of squash and
pumpkin growing in many parts of Utah   The disease, which
resembles bacterial wilt in many respects, is caused entirely by
the feeding activity of the bug, there being no parasitic micro-
organism involved   Under experimental conditions, wilting
occurred in 24 hours to 16 days, depending upon the number of
insects, age of plant, and other factors

If the insects were removed before wilting had progressed too
far, the plants recovered and the new growth was normal
Only the parts above the point of insect feeding were affected
Because of the rapid rate of development and the small number
of insects required to cause wilting, it was concluded that the
disease is caused by the injection of a toxic substance into the
plant by the insect during the feeding process

Insect Galls.—Galls caused by insects constitute a pathological
condition that should be classified with those diseases caused by
toxicogenic insects   It is agreed by nearly all those who have
studied the subject that the galls develop in response to a
stimulating substance introduced into the plant by the insects
In practically all insect galls, the stimulus to abnormal over-
growth arises from the young insects that develop inside the
plant tissues   There is some evidence that the females of certain
gall-producing insects secrete an irritant that is injected into
the plant at the time of oviposition   An enlargement of the
tissue takes place before the egg has hatched, probably as a

result of the injected substance, but the presence of the developing larva is necessary for the complete formation of the typical gall

Cecidiology, or the study of galls, is an extensive subject and has been investigated from many viewpoints The number of insect species that cause galls is very large However, insect galls do not cause a great amount of injury to cultivated plants and consequently have received relatively little attention from the plant pathologists Comprehensive treatments of the subject chiefly from the academic viewpoint, have been written by Cook (1902, 1903, 1904), Connold (1902), Cosens (1912) Felt (1917) Kuster (1925), Ross (1932), and others It will be necessary here to give only a brief outline of the essential known facts about insect galls

A gall, or cecidium, is usually defined as an abnormal plant overgrowth caused by a parasitic plant or animal If caused by a plant stimulus the gall is known as a *phytocecidium*, if caused by an animal stimulus, it is a *zoocecidium* The majority of plant galls are zoocecidia and are caused principally by insects and by mites (*Acarina*), especially by species of *Acarus Eriophyes*, and *Phyllocoptes* The gall-forming insects are found, for the most part, in the Hymenoptera, Diptera, and Homoptera A few minor galls are caused by species of Coleoptera and Lepidoptera Most of the gall-producing Hymenoptera are in the family Cynipidae, although a few representatives of other families also are gall formers According to Folsom and Wardle (1934), approximately 86 per cent of the cynipid galls are found on species of *Quercus*, about 7 per cent on species of *Rosa*, two per cent on the Compositae and the remainder on other species of plants

The Diptera include the large family Cecidomyidae, or gall midges The North American gall midges and their galls have been studied extensively by Felt (1913 to 1925) who has described more than four hundred species forming galls on roots, stems, leaves, fruits, and buds of nearly two hundred genera of plants In addition to the gall midges, a few Diptera of the family Trypaneidae (Trypetidae), Chloropidae (Oscinidae), and Agromyzidae also produce galls

The gall-producing Homoptera are confined mostly to the Aphididae and Psyllidae with a few in the Coccidae The gall

aphids attack a wide variety of plants, and the Psyllidae cause
most of their galls on species of hackberry

Mites belonging to the family Eryophyidae cause leaf and
bud galls   One group of mite galls is characterized by the
excessive production of abnormal trichomes   The diseased
condition is frequently spoken of as "erinose," and the galls
are often called "felt galls "   The trichomes may be free on the
leaf surface or enclosed in pouchlike concavities resulting from
the mite infestation   Other mites of the family infest buds,
causing them to swell but inhibiting normal unfolding, a condi-
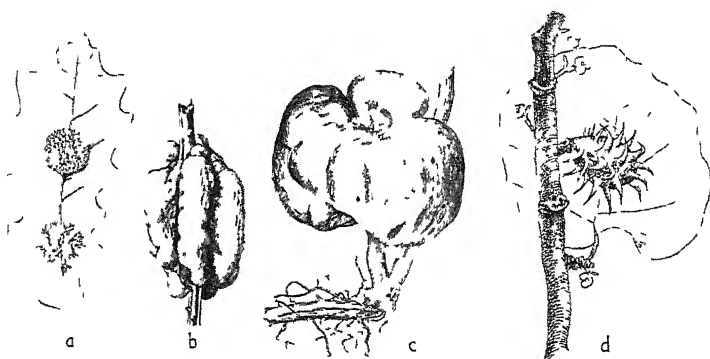tion usually known as "big bud "

Fig 64 —Representative types of insect gall   *a*, a leaf gall of oak caused by
Phlomyx prinoides, b, a stem gall of blackberry caused by *Diastrophus rebulosus,
c*, a root gall of rose caused by *Rhodites radicum, d*, a bud gall of witch-hazel
caused by *Hamamelistes spinosus*   (*After Felt*)

Insect galls assume a wide variety of sizes and shapes   All
gradations from the apparently normal to the decidedly abnormal
are found   It is not easy to draw a line distinguishing true galls
from deformations not worthy of classification as galls   A
definite transition from the simple to the more complex can be
observed   The more simple galls may be formed by a mere
folding of the leaf lamina   More complex sac galls are formed by
invagination of the leaf surface   The more highly developed
cambial galls result from insects developing deep in the tissues
of the stems, usually after the insertion of the egg at time of ovi-
position   The form of the gall and its position on the host plant
are usually very characteristic of the insect, and the species

can often be identified by the character of the gall it produces
Insect galls are often classified on the basis of the part of the plant
on which they characteristically are found   Four classes are
usually recognized (1) leaf galls, (2) stem galls, (3) bud galls,
and (4) root galls (Fig 64)

The physiology and mechanics of gall formation are known
only imperfectly   The detailed structure of many galls and the
insects causing them are known, but the physiological processes
involved in gall production are still obscure   Gall tissues are
formed by hypertrophy or hyperplasia or both   Hyperplasia
is the most common type of tissue change involved in the forma-
tion of insect galls

In nearly all galls, the growth of the gall is associated with the
development of the immature stage of the insect   Certain
Homoptera, especially the aphids, may cause pseudogalls at any
age by external stimulation   A few instances have been
reported where a certain amount of tissue enlargement has
followed oviposition without larval development, but such
stimuli are not sufficient for the formation of a typical gall

It is of interest that alternate generations of certain gall insects
may produce different kinds of galls   Pergande (1901) has
described the life history of *Hamamelistes spinosus* Shimer,
showing that different generations are capable of producing
different kinds of gall on the alternate hosts, while certain genera-
tions of the same species are unable to produce any kind of gall
This phenomenon was discussed by Lutz and Brown (1928),
who pointed out that the agamic generation produces a gall
quite different from that produced by the sexual generation
These may or may not occur on the same plant but never on the
same part of the plant in question   It is generally assumed that
the immediate stimulus is brought about by the secretions of the
developing larvae, although Cook (1902, 1903, 1904) was
inclined to the viewpoint that the mechanical stimulus furnished
by the feeding larvae was sufficient to bring about excessive
growth of the plant tissues   Adler (1881) and Beijerinck (1888)
expressed similar views   Symbiotic microorganisms have been
suspected of being involved also in some cases of gall produc-
tion   Lutz and Brown (1928) found a bacterium constantly
associated with the aphid, *Hamamelistes spinosus*, and the bud
gall of witch hazel   They suggested that the bacteria furnish

the stimulus to gall formation, but they failed to prove this point experimentally

Neger (1913) and others have described a number of midge galls in which certain fungi are constantly associated with the insect   Neger concluded that there is a symbiotic association between the fungus and the insect, and because of the similarity of the association to that of the ambrosia beetles he called the galls "ambrosia galls "

Ross (1922, 1934) has studied extensively a number of these fungus-infected galls   He believes, however, that the fungus lives in the gall as a harmless saprophyte until the larvae mature and emerge, when it becomes parasitic on the plant and causes a decay of the gall   It is not known definitely how the fungi first gain access to the gall tissues, but it is believed that they are carried in by the larvae   The species of fungi and the extent of their development in the galls vary widely   Species of Macrophoma and many yeastlike fungi have been isolated in pure culture   According to Ross, the fungus is not essential to the development of the gall or of the insect   He also does not consider its association with the insect one of symbiosis and objects to calling them ambrosia galls

Docters Van Leeuwen (1929, 1939) has described a gall on *Symplocos fasciculata* Zoll in Java caused by a gall midge (*Asphondylia bursaria* Felt), which he interprets as living in symbiosis with a fungus   When the galls mature in December, the larva within the gall is completely surrounded by a mass of fungus mycelium   The fungus mass is black on the surface but white internally   This internal white portion is completely consumed by the larva before it reaches maturity   The adult insects emerge in February and March and deposit eggs in the stems petioles, and mid-ribs of the leaves   It was observed in a study of the life history of the insect that each egg is constantly contaminated with spores, but the method of contamination was not determined   As soon as the gall tissues are well differentiated, the fungus grows rapidly and fills the entire chamber except the small space occupied by the larva   The gall could not be produced with either the fungus or the insect independently   All attempts to grow the fungus in artificial culture failed   It is not known definitely, therefore, what influence the fungus has on the development of the gall tissues   However,

Docters Van Leeuwen (1939) agrees with Neger that the relationship between fungus and insect is one of true symbiosis and considers the gall an ambrosia gall

Malpighi was perhaps the first to suggest that the stimulus to gall formation was of a chemical nature This conclusion, dating from the seventeenth century, has been reached by many workers of more recent date Rossig (1904), Triggerson (1914), Magnus (1914), Kostoff and Kendal (1930), Zweigelt (1931), and others have presented evidence to support the view that chemical substances secreted by the young insects are the principal stimuli responsible for the abnormal tissue growth There is very little known, however, of the nature of the chemical substances or the mechanism of the changes that they bring about in the plant cells

Cosens (1912) has given consideration to the physiology of gall formation and has concluded

The larva secretes an enzyme capable of changing starch to sugar which acts on the starchy constituents of the nutritive zone and accelerates the rate of their change to sugar The material thus prepared supplies nourishment for both the larva and the gall The protoplasm of the latter is thus rendered unusually active since it receives an abnormal quantity of available food material in a limited area The hypertrophy and cell proliferation and probably the appearance of vestigial issue or other primary characters are the response of the protoplasm of the host to the additional food supply

The experimental proof of the nature of the physiological process is very difficult, and all attempts at artificial production of typical galls by the injection of extracts or other chemical substances have failed Gall production is a very complicated process, and even though simple chemical substances secreted by the insects may be largely responsible for stimulating overgrowth, the presence of the developing larvae appears to be necessary for typical gall production

The relationship between insects and plant diseases in gall formation has been discussed more recently by Felt (1936), who points out that growth in a plant is probably controlled in part by diffusion from one tissue to another and that any single meristematic cell is capable of forming a part of any plant structure normal for the species Potentially, any living

cell is capable of meristematic growth, and its behavior is deter-
mined by its position in the living tissue   Felt concludes

The production of plant galls is dependent on stimulation of plant
cells in a meristematic or plastic condition   A large proportion of plant
galls are produced in buds or in tissues as they develop from buds
The gall producers stimulate cell production in the earlier stages of gall
formation   The possibility of these remarkable developments depends
on the adaptability of plant cells or groups of plant cells   It can hardly
be held that these growths are of material advantage to the plant   They
seem to be, on the part of the plant, a more or less blind reaction of cell
groups, as it were, to stimuli which, under other conditions, might result
in the production of buds and the parts ordinarily developing from
them   There is a close analogy between the insect gall and the develop-
ment of adventitious buds and an actual approach, in methods of
growth and formation, to plant seeds or fruits, the gall producer occupy-
ing the place of the seed and the surrounding tissues being comparable
to the husks or carpels

The histology of insect galls has been studied extensively
The tissue changes associated with gall production may be
either *kataplastic*, in which the gall tissues show little or no
differentiation, consisting mostly of large, thin-walled paren-
chyma cells, or *prosoplastic*, in which the tissues are well differen-
tiated, often being more complex than normal tissues   The
majority of insect galls are prosoplastic   Kataplastic galls are
more commonly produced by fungi and bacteria   In well-
formed, prosoplastic insect galls, three distinct kinds of tissue
may be recognized   protective tissue, mechanic tissue, and
nutritive tissue   The outer tissues made up of epidermal cells
or tissues derived from them are definitely protective in nature
The protective tissues may be little changed from normal or
greatly modified by the excessive production of such additional
protective structures as trichomes   Stomata and lenticels are
present, but the stomata do not close so readily as those on normal
tissue   The mechanic tissue is composed of sclerotic cells
(stone cells) or heavily lignified fibers that surround the develop-
ing larva and protect it from outside pressure   The nutritive
tissue is that immediately surrounding the young insect and the
one from which the larva derives its nourishment   It usually
consists of thin-walled cells with dense protoplasmic contents

In addition to these three tissue types, some galls have the so-called "aeration tissues" composed of loosely arranged cells with large intercellular spaces It has been assumed that such tissues provide for easy access of oxygen to the developing larva Vascular tissue is present in amounts adequate for the needs of the gall and is normal in every respect   An effective vascular system appears to be necessary for the excessive growth required for the development of a prosoplastic gall

Trichomes, glands, and other epidermal structures are often produced in excessive quantities by galls, and many such structures may appear to be new and atypical for the plant species, but, according to Cosens (1912), the galls cannot produce any fundamentally new tissues He states that a careful search of the normal plant has always revealed the structure in question, although it usually occurs in much smaller numbers

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CHAPTER VI

INSECTS AND BACTERIAL DISEASES

Approximately two hundred species of bacteria have been proved pathogenic to plants Some of these are extremely destructive, while others are of minor economic importance Insects play a major role in the epiphytology of several of the most destructive bacterial diseases and influence to some extent the development of many others At least one important bacterial disease, cucurbit wilt, is entirely dependent upon insects for its spread and development

The plant pathogenic bacteria are small, rod-shaped, unicellular organisms averaging less than 1 micron in width and less than 2 microns in length They are unable to penetrate the uninjured cuticle of plants and therefore must gain entrance through natural openings or through injuries The wounds made by insects are utilized for this purpose by many bacterial plant pathogens Bacteria and bacterial diseases have many other characteristics that make them well suited to insect transmission

The literature is replete with references to possible relationships between insects and bacterial diseases When the method of dissemination of a bacterial pathogen is not clearly understood, the statement is very frequently made that it is "probably spread by insects' Such statements usually are not supported by experimental evidence, and often no specific insect is named In other cases, specific insects may be mentioned, but conclusive evidence of their incrimination is often lacking Not all these references are included here In the following pages, some of the better known relationships are discussed, and an attempt is made to weigh the evidence and to evaluate the significance of the insects in the development of the diseases For more complete information on bacterial diseases of plants, the reader is referred to the works of Smith (1905, 1911, 1914), Elliott (1930), and Stapp (1929) and the literature cited by them

Fire Blight of Orchard Fruits —Fire blight is a plant disease of unique historical interest   In 1881, Thomas J Burrill proved that the disease was caused by bacteria, demonstrating for the first time that bacteria could cause a disease of plants   About ten years later, in 1891, Waite proved that bees and wasps were active vectors of the disease   This constituted the first experimental proof that insects were of importance as vectors of any plant disease

Fire blight is chiefly a disease of pears and apples although it is not strictly confined to these crops   Other orchard fruits, as

FIG 65 —Pear blossoms killed by fire blight   (*After Rosen*)

well as many ornamental plants, are often affected, although less severely than pears and apples   The known host range is wide, including, according to Thomas and Thomas (1931) and Thomas and Ark (1934a), 90 or more species mostly in the family Rosaceae   Fire blight is a major disease of apples and pears, and it is a limiting factor in pear production in the Mississippi Valley region of the United States   The disease was first reported in Eastern North America where it has been known since 1794   It is known to occur also in Japan, Italy, and New Zealand

The disease affects primarily the blossoms (Fig 65) and young twigs (Fig 66) of apple and pear trees, but infection may occur

also in laiger bianches, causing destructive cankeis   The cankeis
often completely gudle and kill the laige bianches   When the
tiunk of the tiee is affected, the condition is called "collai blight"
Peai tiees and tiees of the most susceptible vaiieties of apple
may be killed outiight by fiie blight alone   On the moie

Fig 66 —Twig blight of pear   Although infection may occur through stomata
or mechanical injury, twig blight most commonly follows inoculation by sucking
insects   (*After Rosen*)

resistant vaiieties, fire blight itself may be less destiuctive,
but it is fiequently followed by black rot and othei fungus
diseases that eventually destioy the tiee

Fire blight is caused by bacteiia [*Erwinia amylovora* (Buirill)
Winslow *et al*] that are favored by warm, humid weather and
are most virulent on succulent, rapidly growing tissue   Our
knowledge of the epiphytology of fire blight is incomplete, and

there is a wide diversity of opinion among those who have investigated the subject   Early investigators recognized that the pathogen could live over winter in the cankers on the larger branches, and it was generally assumed that these "holdover" cankers constituted the chief, if not the only, means of survival However, in recent years several other possibilities have been suggested   The sources of primary inoculum in the spring and the relative importance of the different means of dissemination of the pathogen constitute the crux of the fire-blight problem

As early as 1884, Forbes observed fire-blight lesions associated with the feeding activities of the tarnished plant bug (*Lygus pratensis* L) and expressed the opinion that this insect was acting as a vector of the disease   Forbes, however, presented only observational evidence for his conclusions   The accuracy of his observations was confirmed by experimental evidence presented by Stewart (1913*a*, 1913*b*) nearly thirty years later

Waite (1891) proved experimentally that bees and wasps become contaminated with the fire-blight pathogen when visiting blighted pear blossoms and that these insects commonly spread the infection to other blossoms   The most complete account of Waite's work is given by Smith (1911, Vol II, p 55) who states·

Mr Waite again produced blossom-blight on certain clusters of pear-blossoms by infecting the floral nectaries and by allowing the bees to have free access to these blossoms   He succeeded through their agency in transmitting blight to other flower-clusters on the same tree   One of these experiments took place on the grounds of the United States Department of Agriculture, an isolated tree previously free from blight being used for this purpose   Bees were observed to visit the infected flowers and, subsequently, flowers on other clusters, which flowers afterwards blighted   Some of these bees were caught, their mouth parts excised, and cultures made therefrom by means of poured-plates in Petri dishes   Colonies obtained in this way closely resembled the pear-blight organism, and inoculations therefrom produced the disease in sound pear-shoots, thus demonstrating beyond dispute the actual presence of the pear-blight organism on the mouth parts of the suspected bees

Everybody connected with the plant pathological work of the United States Department of Agriculture at that time had knowledge of these results   The writer, among others, saw all of the experiments described and knows that they were well done and that the above brief outline can be accepted as an accurate statement of what actually took place

Being familiar with the holdover cankers and the bacterial exudate frequently associated with them in early spring (Fig 67), Waite concluded that bees, wasps, and other insects visit the exudate, become contaminated with the bacteria, and disseminate them to the blossoms   But this conclusion was not based on experimental evidence   All his experiments were concerned with the spread of secondary inoculum   Conclusions
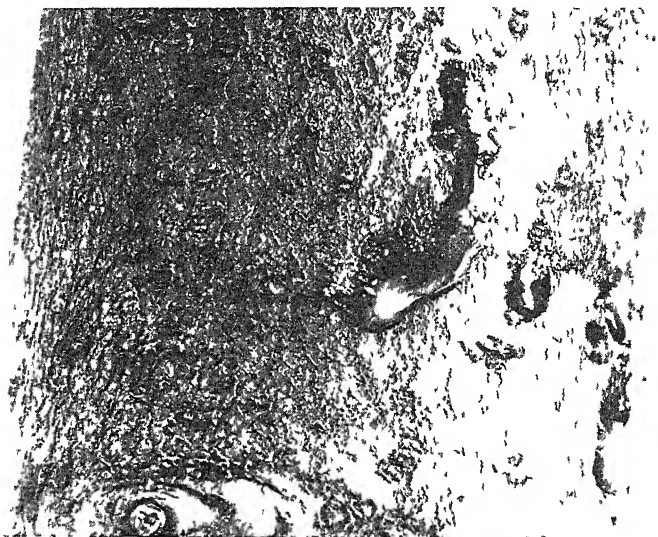

Fig 67 — A holdover canker of fire blight on apple showing the bacterial ooze, from which much blossom infection originates   Flies and ants feed upon the ooze and transfer the bacteria to blossoms where they infect   Secondary spread is accomplished largely through the activities of the honey bee   Rain water is also important in both primary and secondary spread of blight   (*After Whetzel*)

concerning primary infection were based on observation and assumption only, and later work indicates that bees rarely visit the exudate   Writers, in reporting Waite's work, often have accepted the assumed role of bees in primary infection as a proved fact   and this explanation was accepted generally for many years   Recently several workers have questioned the importance of holdover cankers in primary infection and offered alternative theories based on more or less experimental evidence   On the other hand, Thomas and Ark (1934a) have reported direct experimental proof that flies and ants carry blight bac-

teria from holdover cankers to blossoms and initiate primary infection

Gossard and Walton (1922) were the first to emphasize the importance of rain drip and wind-blown rain as a means of dissemination of secondary inoculum, but they did not appreciate its possible significance in primary infection   These workers, by means of cage experiments proved conclusively the effectiveness of rain in disseminating the bacteria from blossom to blossom   They verified the earlier work of Waite showing that bees are vectors, but they considered rain to be the most important agent of dissemination after a few centers of primary infection had been established by insects   The proof of the importance of rain water in primary infection has been demonstrated by Brooks (1926) and confirmed by Miller (1929), Tullis (1929), and others who maintain that the greater part of primary infection results from inoculum from "holdover" cankers splashed or blown to blossoms in rain water   Thomas and Ark (1934*b*), on the other hand, claim that rain water is of little importance in actual dissemination but that it has an indirect effect in providing favorable conditions for infection after dissemination by insects has taken place   They point out that in dry weather the nectar in blossoms is too concentrated for growth of the bacteria and that the more dilute nectar occurring in rainy weather is more conducive to infection   Another indirect effect of rainfall is pointed out by Shaw (1935) who has shown that apple and pear shoots are more susceptible in wet weather because of the increased intercellular humidity which is favorable for infection and development of the disease   Pierstorff (1931) concluded, "Meteoric water did not appear to spread the blight bacteria from blossom to blossom "   Similar conclusions were reached by Parker (1936)

Gossard and Walton (1922) recognized the wide host range of the disease and proposed a new theory to account for primary infection without the aid of holdover cankers   This is the theory that the blight may be spread from the far South by insects and rain from blossom to blossom in a progressive wave northward   After such a wave had started in the South, it would spread progressively northward with the seasonal advance, infecting all orchards in its path, making the presence of holdover cankers relatively unimportant   The theory obviously

is not easily subjected to experimental proof and is not generally accepted

Because of their feeding habits, bees are concerned primarily, if not solely, with blossom infection and do not account for the infection of shoots and twigs that do not bear blossoms Jones (1909) and Whetzel and Stewart (1909) were the first to offer an explanation for twig and shoot infection These workers observed the frequent association of aphids with blighted twigs and concluded that they were the vectors, but no experimental evidence was presented

A few years later, Merrill (1915) reported a similar correlation between aphid infestation and fire-blight infection Stewart (1913a, 1913b) presented the first experimental proof of aphid transmission of fire blight and confirmed the early observations of Forbes that the tarnished plant bug is a vector Later, Stewart and Leonard (1915, 1916) presented evidence that several other sucking insects could serve as vectors They concluded that the mode of transmission was purely mechanical and that any sucking insect feeding on a susceptible host was a potential vector Workers in general agree with this conclusion, but some, including Tullis (1929) and Miller (1929), maintain that sucking insects play a very unimportant part in the epiphytology of fire blight

Much of the earlier work led to the conclusion that, with the exception of blossom infection, the bacteria could enter only through wounds Since the most frequently occurring wounds on young shoots are those made by insects, it was only natural to attribute twig blight to this method of infection However, in 1915 Heald showed that the infection of leaves through natural openings (stomata and hydathodes) was common in the state of Washington and suggested that this might explain many infections which have been attributed to insect inoculation Infection of young leaves in the absence of wounds was verified by Tullis (1929), Miller (1929), and Rosen (1933)

Infections of the larger branches and trunks usually are the result of invasion directly from infected small shoots, but Jones in 1909 demonstrated that such infection often followed the attack of the fruit-tree bark beetle (*Scolytus rugulosus* Ratz) Two years later (1911), he presented definite experimental proof that these insects were important vectors of the disease in

young pear orchards Orton and Adams (1915) observed that 90 per cent of the cases of the "collar blight" type of fire-blight infection on apples in Pennsylvania were associated with infestations of the bark beetle and considered this insect as a possible vector although their conclusions were based largely on observational evidence

Gossard (1916) appears to have been the first to investigate the role of the beehive in the epiphytology of fire blight He found that the fire-blight bacteria could survive for at least 72 hours in honey taken from the hive and concluded that the hive could serve as a distributing center for the fire-blight pathogen during the blossoming period Later Gossard and Walton (1922) demonstrated the presence of the pathogen on the mouth parts of bees entering and leaving the hives They also successfully inoculated apple twigs with honey taken from the hives at the same time Thomas in 1930 showed that the pathogen could survive in the hive on the comb and frames for 55 days and pointed out the danger of translocating hives from one orchard to another

These experiments incriminated the hive as a factor in secondary inoculation, but there was no conclusive evidence that the pathogen could survive the winter in the hive The latter possibility was seriously investigated first by Rosen who, in 1930, reported that he had "successfully isolated the fire-blight pathogen from beehive material gathered throughout the summer, winter, and early spring and from the bees themselves obtained from the hives in the early spring prior to the development of blight " Rosen (1933) obtained 21 successful infections out of 3,534 inoculations into young pear twigs with inoculum obtained from the interior of beehives He pointed out that, in Arkansas, fresh infectious exudate was absent prior to the appearance of blossom blight, which was invariably the first blight to appear, and that blossom blight was abundant in years when there was no rainfall during the blossoming period These facts led him to consider the hive as a significant source of primary inoculum

Rosen's conclusions are questioned by Pierstorff and Lamb (1934), who were unable to produce blossom infection by placing hives artificially infested with the pathogen under apple trees, all enclosed within cheesecloth cages Thomas and Ark (1934a) in California were unable to confirm Rosen's claims that the

pathogen could survive the winter in the hive   They claim
that there is not enough evidence to justify the conclusion that
bacteria taken into the hive by bees are sources of either primary
or secondary inoculum   These workers conclude that, in Cali-
fornia, primary infection originates from bacteria carried from
holdover cankers to blossoms by ants, aphids, beetles, codling
moths, flies, wasps, and yellow jackets (Fig 68)   Parker (1936)
also concluded that the pathogen probably could not survive the
winter in the beehive and attributed primary infection to inoc-
ulum transferred by ants and flies to blossoms from holdover
cankers

Further objections to Rosen's theory were raised by Hilde-
brand and Phillips (1936), who have made the most thorough
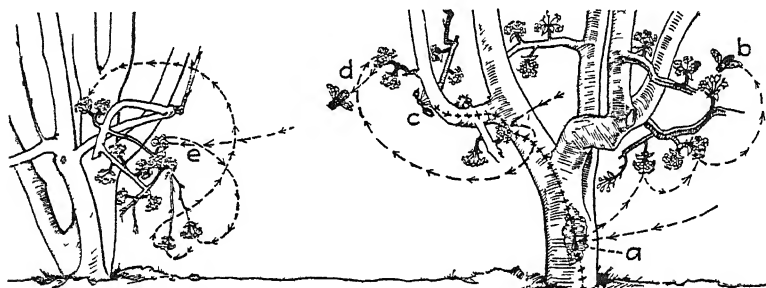
Fig 68 —A diagrammatic sketch showing the relation of insects to the spread
and development of fire blight   *a,* oozing cankers from which flies (*b*) and ants
(*c*) transport bacteria to blossoms and initiate primary infection, *d,* bees and
other insects that transport bacteria from blossom to blossom, inducing secondary
infection   (*After Thomas and Ark*)

study yet reported of the relation of the bee and the beehive
to the epiphytology of fire blight   They were unable to recover
the pathogen from honey, comb, or bees after 3 days, when the
pathogen was introduced by feeding the bees on a 60 per cent
sucrose solution heavily charged with the bacteria   The longest
period of survival in the hive that they could demonstrate was
13 days in pollen and 12 days in frame scrapings   After pointing
out that none of the individual worker bees active during an
epidemic of blossom blight would be likely to survive until the
following spring, they attempted to isolate the pathogen from
the eggs, larvae, pupae, and the adult bees in colonies fed on
sugar solutions containing the bacteria, but were unsuccessful
It was proved that the bee was important in disseminating the

inoculum from flower to flower and, provided that the bees were feeding on contaminated food, from hive to flowers It was concluded, however, that the pathogen was incapable of over-wintering in the beehive on the comb, in the honey, or in association with the bee, and that the hive was not a source of primary inoculum in the spring of the year

This brief review reveals a wide diversity of both opinion and evidence concerning the importance of insects in the epiphytology of fire blight It is somewhat ironical that the first association between insect and plant disease to be established should, after 50 years, remain in such an uncertain and unsatisfactory state There are several reasons for this The nature of fire blight makes experimentation difficult, the size of the suscepts makes caging experiments expensive and greenhouse experiments very unsatisfactory, and the widely different environmental conditions pre-vailing in the different regions where the investigations have been made may explain some of the divergent results

Much of the work to date has been done with the assumption that the pathogen does not survive in the soil, but recent evidence presented by Ark (1932), that the pathogen may survive for a considerable length of time in the soil, opens up new possibilities that should be thoroughly studied Hildebrand (1937) has shown that small numbers, even single cells of *Erwinia amylovora,* are highly infectious when inoculated into nectar of apple flowers He emphasizes the potential infective power of a very small number of bacteria when disseminated by bees from blossom to blossom The evidence available is sufficient to convince anyone that insects do play an important part in the spread and development of fire blight, but it is practically impossible to evaluate the relative importance of insects and other factors as well as the relative importance of some of the different species of insects that have been incriminated Much more investigation of the subject is needed The investigations should have as their main objective the solution of these specific problems and should not be carried out merely as an incidental part of more inclusive studies They should be made by investigators thoroughly familiar with the techniques of both entomology and plant pathology and with a knowledge of the various associations of insects with plant diseases The recognized importance of the bee in the pollination of fruits and the increasing attention being given to the control of

blossom blight in orchard practice (Hildebrand 1937a) make it imperative that the relation of bees to the initiation of fire-blight epiphytotics be definitely and accurately established   The problem must be approached with an open mind   The investigators must be thoroughly familiar with the life history, habits, anatomy, and physiology of bees and must have an adequate conception of the nature of the disease and its cause

Recent work has placed increasing emphasis on flies as agents of dissemination of primary inoculum from holdover canker to blossoms (Thomas and Ark 1934 and Parker 1936)   In view of this fact, the work of Ark and Thomas (1936) is very significant By controlled laboratory experiments, they have shown that the fire-blight pathogen may live for several days in the intestinal tract of *Drosophila melanogaster, Musca domestica,* and *Lucilia seriata*   Eggs of *M domestica* from contaminated females were externally contaminated with the pathogen   It was shown also that when the larvae of *D melanogaster* and *M domestica* were fed on contaminated food the pathogen persisted through the puparia and recontaminated the emerging adult   The habit that these insects have of regurgitating the contents of the crop when feeding would make them especially effective as vectors of the fire-blight pathogen   The survival of the bacteria in the puparia opens up the possibility of the pathogen overwintering in this way and suggests another possible source of primary inoculum   These possibilities need further investigation under orchard conditions

Soft Rot of Plants and Dipterous Insects —The relation of dipterous insects to the bacterial soft rot of plants constitutes one of the most interesting associations between insects and plant diseases   The relationship was first discovered in a study of the seed-corn maggot as a factor in the development of the blackleg disease of potatoes (Leach 1925, 1926), and it has since been demonstrated for several other insects and plant diseases (Bonde 1930a, Johnson 1930, Leach 1927)

Potato Blackleg —Blackleg is one of the major diseases of the potato   It causes an average annual loss of approximately 2 per cent of the crop   In badly affected fields the loss may be 50 per cent or more, and it is not uncommon to find fields in which 10 to 15 per cent of the plants have been killed by the disease   In the majority of the fields, however, the losses are seldom greater than 5 per cent of the crop   In addition to reduced yields, there may

be further losses caused by decay of the tubers in storage or in transit This is especially true where good storage conditions are not possible

Blackleg is a bacterial soft rot caused by *Erwinia carotovora* (Jones) Winslow *et al* Any part of the potato plant may be affected, although it is generally the seed pieces, the base of the stem, and the tubers that are directly infected by the bacteria (Fig 69) The infected seed pieces are usually decayed throughout before the bacteria spread into the stem or out into the stolons to the newly formed tubers Seed pieces destroyed by blackleg

Fig 69 —Potato blackleg   *A*, a potato plant drooping and beginning to die from blackleg infection compared with a healthy plant of the same age, *B*, an affected plant pulled up showing the dark-colored soft rot of the base or the stem   The seed piece has been completely decayed

vary in appearance   In the majority of cases, the pathogenic bacteria are accompanied or closely followed by many saprophytic bacteria and fungi that reduce the seed piece to a slimy, foul-smelling mass in which the larvae of insects, particularly the seed-corn maggot (*Hylemyia cilicrura*) frequently may be found On the other hand, especially late in the growing season, the seed piece may be affected by a watery translucent decay with no unpleasant odor   In such cases, relatively few saprophytes are present

When a plant becomes diseased after tubers have been formed, the decay frequently spreads through the stolons and into the new

tubers   In wet and heavy soils, these may be completely
destroyed before harvest   In light or very dry soils, usually a
small portion of the stem end of the tubers will be decayed, or
perhaps only a browning of the vascular bundle may result   The
flesh of tubers rotted in the soil as a result of stolon infection may
remain nearly as white as normal until cut open and exposed to
the air, when it will rapidly turn brown or black   Tubers
decayed by a pure culture of the blackleg bacteria do not have an
unpleasant odor, but when secondary organisms are present a foul
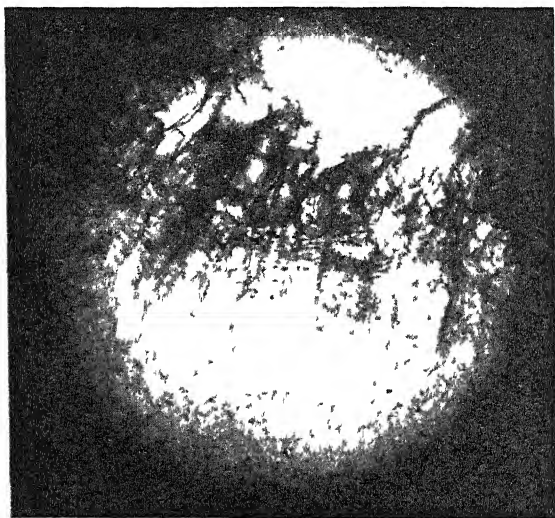
Fig 70 —A section through a lesion caused by blackleg on a potato tuber
showing the wound cork that has successfully checked the decay and walled off
the bacteria from the healthy tissues

odor may result   For a long time, the bacteria causing blackleg
of potatoes were thought to be different from those causing soft
rot of other vegetables, but more recent work has demonstrated
them to be the same (Leach 1930*b* and Bonde 1939*a*)

For many years, there was a general belief that the bacteria
causing blackleg could not survive in the soil over winter   This
belief was based partly on the negative results obtained by
Rosenbaum and Ramsey (1918) and Ramsey (1919) and partly
on a misunderstanding of the factors influencing infection of
potato plants by blackleg   More recently it has been shown
that the conclusion based on the earlier work was not justified

and that the bacteria do survive in the soil (Leach 1930a) In fact, the bacteria are present in most cultivated soils and may infect potato seed pieces when conditions are favorable When potato seed pieces are planted in a soil under conditions favorable for growth, a layer of cork cells is formed over the cut surface and serves as an effective barrier against bacterial infection (Fig 70) Infection cannot occur unless some condition prevents the formation of this cork layer or enables the bacteria successfully to pass through it

There are several ways in which the bacteria may succeed in penetrating this protective layer of cork Numerous experiments have shown that, if the supply of oxygen is low, cork cells cannot be formed In very wet soils, the air spaces are filled with water, the air being thus forced out, the supply of oxygen is limited Leach (1930a) has shown that cork formation is greatly inhibited when tubers are planted in very wet soils, but this has no retarding effect on the growth of the bacteria The bacteria are facultative anaerobes and are able to grow as well in the absence of oxygen as in the presence of abundant oxygen Under anaerobic conditions, cork cannot be formed by the tubers, but the bacteria may grow rapidly Thus there are produced conditions favorable for infection of seed pieces by bacteria in the soil This in all probability accounts for the commonly observed fact that blackleg usually is more prevalent in wet seasons than in dry seasons It may also explain the greater prevalence of blackleg on heavy, poorly drained soils as compared with lighter well-drained ones

Insects may aid the bacteria in penetrating the protective cork layer formed by the seed pieces Investigations by Leach (1926) resulted in the discovery that the seed pieces of plants affected with blackleg were frequently infested by larvae of the seed-corn maggot (*Hylemyia cilicrura* Rond) Further studies led to the conclusion that this insect is an important agent of dissemination and inoculation of blackleg Bonde (1930b) has shown that a closely related species (*H trichodactyla* Rond) also serves in the same capacity

The seed-corn maggot is a common pest of the potato and many other plants Reports of injury on corn, beans peas, turnips, cabbages, radishes, onions beets, potatoes, hedge mustard, tomatoes, and several other plants occur in the literature The insect

oveiwinters in the soil in the pupaiial stage   The adult flies emeige in eaily spiing   They may be seen flitting about ovei the suiface of the giound in great numbeis duiing the planting season and appeai to be attracted by the fieshly tuined soil   They aie about the size of a housefly, which they iesemble in many iespects (Fig 71)   Eggs are deposited on, oi in, the soil neai seed pieces and young potato plants (Fig 72)   The eggs aie slightly less
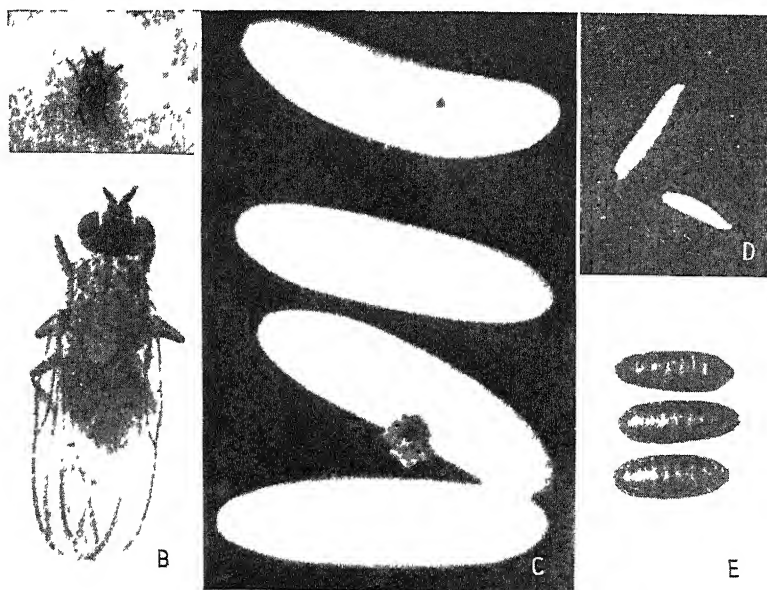
Fig 71 —The seed-corn maggot (*Hylemyia cilicrura*), the vectoi of potato blackleg and bacterial soft rot of othei plants   *A*, an adult female fly iesting on the surface of a potato tubei (appiox $1\frac{1}{2}\times$), *B*, a female fly (appiox $9\times$), *C*, four eggs (appiox $100\times$), *D*, two larvae (appiox $2\times$), *E*, thiee pupae (appiox $3\frac{1}{2}\times$)

than $\frac{1}{25}$ inch in length but may be seen ieadily with the naked eye   They aie slightly cuived, white, and distinctly ieticulate (Fig 71*C*)   When fieshly deposited, they aie coveied with a sticky fluid that causes them to adheie to anything with which they come in contact

The eggs hatch aftei 2 or 3 days   The maggot, upon emer-gence, is nearly transparent and only slightly longer than the egg, but it is able to move about rapidly in seaich of food   The mouth of the maggot is equipped with two black, sharp, clawlike structures with which it is able to penetrate the tissues of the seed

piece   Observations have shown that the maggots during the
first 24 hours will crawl about over the cut surface of the seed
piece scraping with their mouth parts until the tissues begin to
decay   During the next few days, they penetrate deep into the
tissues, thoroughly inoculating the seed piece with bacteria
Experiments have demonstrated that the eggs are sometimes
contaminated on the surface with the blackleg bacteria when
deposited   It has been shown, also, that the bacteria can survive
in the soil   The maggot, therefore, may pick up the bacteria
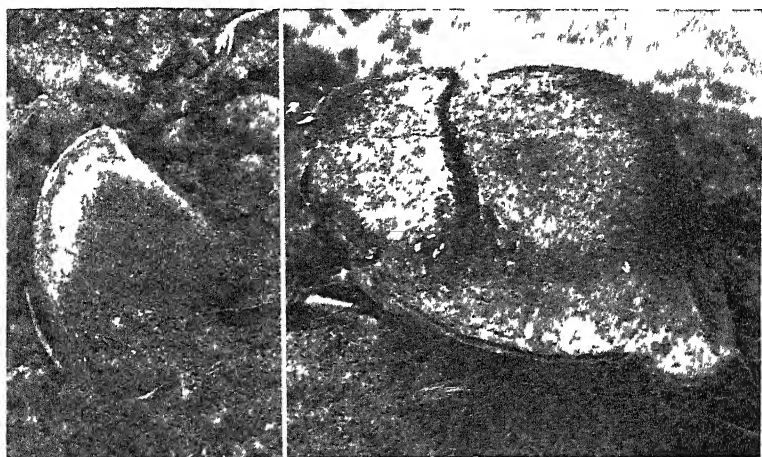
Fig 72 —Eggs of the seed-corn maggot on, and in the soil near potato seed
pieces   Photographed 3 days after planting

from the egg shells, from the soil, or perhaps from the surface
of contaminated seed pieces   The maggot thus acts as a very
effective agent of inoculation   By the continued burrowing of
the maggot, any tendency of the tissues to form wound cork is
thoroughly overcome

No effective method of controlling these insects is known,
although certain cultural practices may reduce the damage done
by them (Leach 1931*a* and Bonde 1930*b*)   Bonde (1930*b*, 1939*b*)
has shown that the young maggots are attracted to small super-
ficial bacterial lesions on the cut surface of potato seed pieces and
that they become established through such lesions more easily
than through a sound well-suberized surface   These lesions are
usually caused by nonpathogenic or very weakly pathogenic

bacteria that are not capable of causing a general necrosis of the seed pieces or blackleg

After 2 or 3 weeks' development in the seed pieces, the maggots reach their maximum size of about 7 to 8 mm   They then leave the seed piece, enter the soil, and pupate   In the meantime, the seed piece is usually completely decayed, and the bacteria are invading the stems of the plants, producing typical symptoms of blackleg   Pupation is usually well under way by the time the first aboveground symptoms appear   The puparia are about
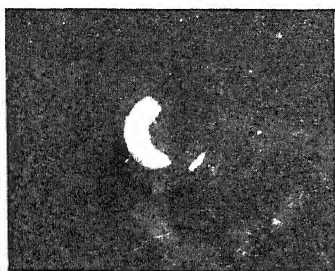
FIG 73 —Two larvae of the seed-corn maggot showing the effect of bacteria on growth   Both larvae are the same age and were hatched from surface-sterilized eggs   The small one on the right was grown for 12 days on a sterile potato plug The larger one was grown on a similar potato plug infected with bacteria   1½ ×

⅛ inch in length and somewhat oval in shape (Fig 71e)   They vary from light brown to dark reddish brown according to age The duration of the pupal stage varies from 7 to 14 days in summer

There are usually two broods of the insect on potatoes   The first brood is the more important in its relation to blackleg, for the eggs are deposited near seed pieces or young potato plants   The second brood usually deposits its eggs near or on the stems of plants already affected with blackleg   The maggots of the second brood may frequently be found in the stems of blackleg plants, while the maggots of the first brood are confined chiefly to the seed pieces

The symbiotic relationships between bacteria and the seed-corn maggot have been studied by Leach (1931b, 1933)   It was found that the normal bacterial flora of the intestinal tract of both the larvae and the adult flies is made up of several morphologically and physiologically similar species of bacteria   The most common bacteria are species closely resembling *Pseudomonas fluoresense* Migula and *Ps nonliquefaciens* Bergey *et al*   *Erwinia carotovora* is frequently but not always present   These species are regularly passed uninjured through the intestinal tracts of both larvae and flies   It was shown, also, that these bacteria may survive in the puparia and emerge with the adult fly   In the imago, certain species ingested with the food are destroyed and digested while certain others are uninjured   Some of these

actively grow and multiply in the intestinal tract   In neither larva nor imago are the bacteria harbored in special organs such as those described by Petri (1910) and Stammer (1929) in *Dacus oleae* and other Trypetidae

Nutritional studies (Leach 1926, 1931*b*, Huff 1928) indicate that the bacteria aid the development of the larvae by transforming the plant tissues into a form more readily assimilated The larvae do not develop normally on sterile potato tubers or on sterilized bean seed but will grow normally if these are contaminated with the bacteria usually associated with the
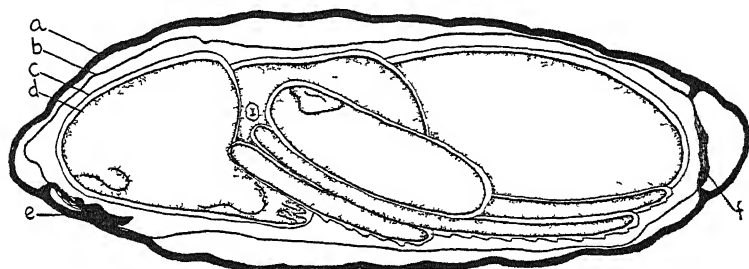
FIG 74 —A sketch of a puparium of the seed-corn maggot showing the pupa in perspective, and the various enveloping layers in section   *a* puparium shell, *b* prepupal cuticle *c* pupal cuticle *d* pupa, *e*, extruded lining of fore-intestine of larva *f* extruded lining of larval hind-intestine   Approx 35 ×

insect (Fig 73)   They grow normally on seeds that have been partly decayed by bacteria and then sterilized by heat   The larvae will grow slowly and pupate also on sterile germinating bean seed, indicating that the bacteria, as such, are not essential but that they are needed when the larvae are feeding on non-germinating plant tissues   The specific changes that are essential for the utilization of plant tissues by the larvae are not known   This problem should be investigated further with suitably refined techniques

Leach (1933) has shown that the bacteria survive in three different locations in the puparium   in the cast-out linings of the fore-intestine, in the cast-out linings of the hind-intestine, and in the lumen of the mid-intestine of the pupae (Fig 74) The bacteria that survive in the first two localities are those that happen to be in the fore- and hind-intestines at the time of pupation and may be of several different kinds   Those surviving in the mid-intestine are reduced to relatively small

numbers during histolysis but increase rapidly just before the emergence of the fly from the puparium (Figs 75, 76, and 77) There seems to be a selective action on the bacteria surviving in the mid-intestine that is not operative on those surviving in the cast-off linings of the fore- and hind-intestines   Those surviving in the mid-intestine appear to be of one kind   The specific identity of the bacteria surviving in the mid-intestine has been determined in only a few cases, in all of which a single species of a nonpathogenic bacterium resembling, but not identical with *Ps fluoresence*, was found

FIG 75 — A section through the mid-intestine of a seed-corn maggot larva in early stages of pupation showing the contracted lumen and the cast-off epithelial cells   Practically all the food material has been eliminated, and only a few bacteria remain

Insect inoculation and direct infection from the soil constitute two sources of infection that may result in severe outbreaks of blackleg without regard to the source of the seed stock   Nevertheless, the disease may be transmitted through infected seed pieces, and this source of infection should not be disregarded When a plant becomes affected with blackleg late in the season and is not killed until after tubers have formed, it is frequently found that the decay has extended through the stolons and has entered the tubers through the stem end   Such tubers usually are not completely decayed but remain sound with the exception of a slight depression at the stem end and a browning of the
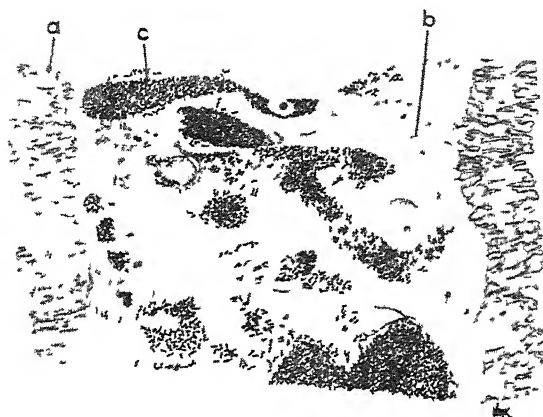
Fig 76 — A camera lucida sketch from a stained slide showing the contents of the mid intestine of a pupa of the seed corn maggot   *a* the embryonic cells of the new mid-intestine wall *b* the epithelial cells of the old larval mid-intestine being sloughed *c* living bacterial cells   Approx 250×
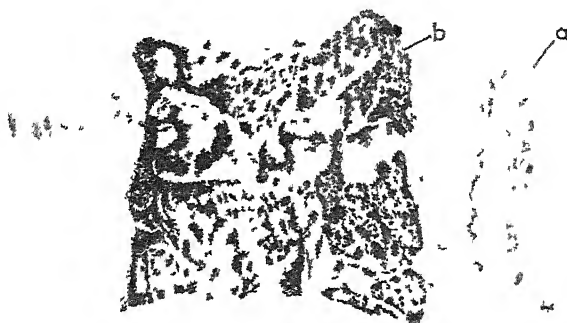
Fig 77 — A camera-lucida sketch from a stained slide showing a section of the hind-intestine of a freshly emerged imago of the seed-corn maggot   *a* wall of hind-intestine *b* residue of disintegrated epithelial cells *c* the bacteria which have survived through metamorphosis and are multiplying on the disintegrated epithelial cells   Approx 250×

vascular bundles for some distance beyond   Experiments
have shown that the bacteria may live over in tubers infected
in this way, and such tubers frequently give rise to blackleg
plants   Tubers infected in this manner appear to be less effective
in walling off the bacteria than those inoculated through the
cut surface at planting time   Experiments have shown that
only a relatively small percentage (10 to 15 per cent) of such
stem-end infected tubers are likely to produce blackleg plants
Therefore, when we consider the number of tubers likely to be
infected in this way in a given lot of seed tubers, it appears
extremely unlikely that this source of infection could result in
more than a very small percentage of the infection frequently
found in potato fields

Soft Rot of Crucifers and the Cabbage Maggot —Crucifers,
in common with many other plants, are subject to bacterial
soft rot   The disease is very commonly associated with the
attacks of the cabbage maggot (*Hylemyia brassicae* Bouche)
Entomologists have frequently mentioned decay of the tissues
following maggot injury, but the significance of the association
was not known until demonstrated by Johnson (1940) and Bonde
(1930a), who proved that the insect was a common vector of
the soft-rot bacteria

Soft rot may affect different species of crucifers in several
different ways   One of the most common and most destructive
manifestations of the disease is the so-called "stump rot" of
cabbage, a decay affecting plants that have started to "head
out "   The decay originates in the stem but eventually spreads
into the base of the head   The first noticeable symptoms
usually consist in a wilting of the outer leaves and a cessation of
growth   When viewed casually, the head may appear healthy,
but further examination will reveal that the interior of the stem
is decayed and that the head can be separated readily from the
stem, leaving a rotted stump

This infection practically always originates at the point of
maggot attack   This may be below ground, in which case
the decay follows the tender tissues of the pith inside the hard
vascular ring and may escape observation until the base of the
head is thoroughly decayed   In other cases, the decay may
originate at the base of the older leaves where the later broods
of flies frequently deposit their eggs   Maggot attack does not

always result in stump rot   In many cases, the decay is con-
fined to the succulent tissue of the cortex outside the hard
lignified vascular cylinder, and the tissues soon heal

The symbiotic relations between the bacteria and the insect
seem to be essentially the same as those described for the seed-
corn maggot   This insect has been mentioned also as a possible
vector of *Phytomonas campestris* (Pammel) Bergey *et al*, the
cause of the black rot of cabbage, but adequate proof is lacking

Heart Rot of Celery —Bacterial soft rot caused by *Erwinia
carotovora* (Jones) Bergey *et al* is destructive on celery chiefly
as a heart rot   Heart rot was first recognized and adequately
described by Wormald (1914, 1917)   Soft rot may affect any
part of the celery plant but on the older, outer leaves it is of
little significance because these are discarded before the celery
is packed for market   But when the heart leaves are affected,
the central bud is destroyed, the stem elongates, and the plants
become unmarketable (Fig 78)   Heart rot should not be con-
fused with blackheart, a nonparasitic disease, which sometimes
may be followed by soft rot (Foster 1934)

Weather conditions have a profound influence on the develop-
ment of heart rot   The influence, however, is contrary to that
generally prevailing for the disease on other plants   Destructive
outbreaks of celery heart rot occur only in hot dry weather,
whereas soft rot of most other plants is favored by rainy weather
and high humidity   The explanation of this apparent anomaly
is found in the dependence of the disease upon the activity of
certain dipterous insects   Two species of leaf-mining Diptera
(*Scaptomyza graminum* Fall and *Elachiptera costata* Leow)
are vectors of the disease (Leach 1927)

These insects deposit their eggs on the leaves of the celery
and the young larvae burrow into the leaves   The soft-rot
infection starts at the point of entrance of the larvae   The
insects normally deposit their eggs in places where the relative
humidity is high, and when the eggs hatch the larvae search
for a moist place   Observations show that they penetrate the
leaf most often where there is free water on the leaf surface
In moist weather, nearly all the eggs are deposited on the older
outer leaves   These leaves are more resistant to decay and
if decay does result the outer leaves may be destroyed with no
appreciable loss to the grower   In dry weather, the insects

deposit their eggs on the inner heart leaves where the humidity is always high even in the warmest weather.   The succulent heart leaves are very susceptible, and the decay develops rapidly until the terminal bud is killed and the plant is a total loss. This disease is prevalent in Great Britain, and the association

FIG 78 —A celery plant affected with heart rot caused by *Erwinia carotovora* and transmitted by Dipterous insects, the most important of which are *Scaptomyza graminum* and *Elachiptera costata*

between *S graminum* and the soft-rot bacteria has been confirmed by Ogilvie, Mulligan, and Brian (1935).   The course of the bacteria in the bodies of these insects has not been studied. It is assumed that the association is somewhat similar to that of the seed-corn maggot, but the facts must await investigation.

Richardson (1938) has shown that the tarnished plant bug (*Lygus pratensis* L) also may serve as an agent of inoculation for

celery heart rot   The insects were allowed to feed on celery plants that had been sprayed with a water suspension of *Erwinia carotovora* and incubated in high humidity   Under these conditions, infection occurred in the feeding punctures within 48 hours Control plants treated in the same way but not subjected to the insects remained healthy except where artificial wounds were present   Since plants sprayed with sterile water and subjected to the insects remained healthy, one would conclude that under natural conditions the tarnished plant bug would be less effective as a vector than the Dipterous insects

Bacterial Wilt of Cucurbits —Cucurbit wilt was first described by Erwin F Smith in 1893   It is confined to the family Cucur-

Fig 79 —A squash plant affected with bacterial wilt, a disease transmitted in nature only by two species of cucumber beetle

bitaceae but apparently does not affect all members of the family Cucumbers are most frequently affected, followed in order of susceptibility by cantaloupes, summer squash, winter squash, and pumpkins   Watermelons are said to be immune or very highly resistant   Bacterial wilt is widespread throughout the eastern part of the United States and has been reported from Europe, South Africa, and Japan   Its prevalence varies from year to year, and it is often very destructive killing more than half the plants in some fields   Affected plants droop as from the lack of water (Fig 79)   One or more runners may wilt depending upon the point of inoculation   In early stages of infection the plants may droop during mid-day and revive over night only to droop more severely the next day and collapse completely

Bacterial wilt is caused by *Erwinia tracheiphila* (Erw Smith)
Winslow *et al* , a white, viscid, capsulate bacillus   The pathogen
is a strict vascular parasite, being confined almost entirely to
the vascular bundles of affected stems   The white viscid mass
of bacteria that exudes from the vascular bundles, when an
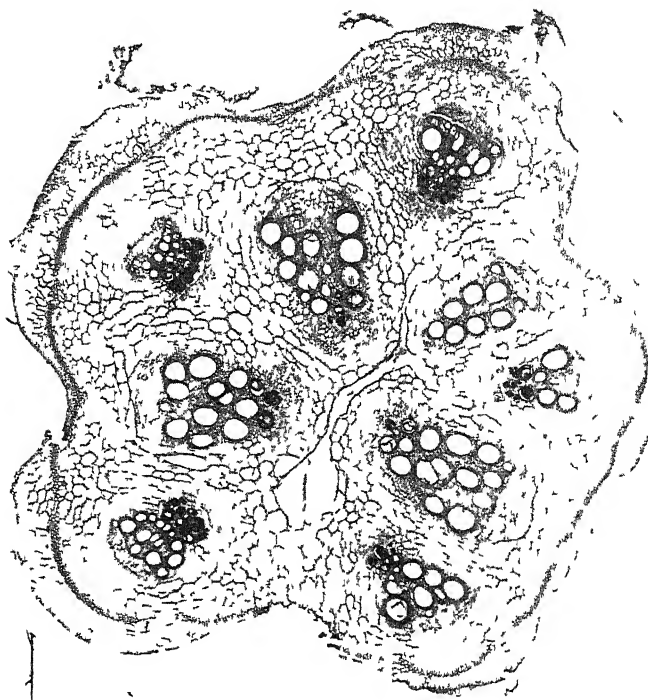
FIG 80 — A cross section of a cucumber stem infected with bacterial wilt
showing the spiral vessels occluded by masses of *Erwinia tracheiphila*   Approx
12 ×   (*Photograph courtesy Bureau of Plant Industry, U S Department of
Agriculture*)

infected stem is cut, is the best diagnostic symptom of the disease
Wilting is caused largely by occlusion of the tracheal tubes
(Fig 80)

E F Smith in 1911 expressed belief that the disease is dis-
seminated by insects, especially the striped cucumber beetle
(*Diabrotica vittata* Fabr) (Fig 81)   The first experimental proof
was submitted in 1915 by Rand, who incriminated also the

twelve-spotted cucumber beetle (*D duodecimpunctata* Oliv)
(Fig 82)   These two insects are the only known vectors of the
disease, and no other natural means of spread has been reported
Rand and Enlows (1916) have shown by careful experiment
that infection does not come through soil or seed and that the
following insects are not vectors the squash bug (*Anasa tristis*
De G), the squash ladybird (*Epilachna borealis* Fabr), the melon
aphis (*Aphis gossypii* Glov), the honeybee (*Apis mellifera* L)
and the potato flea beetle (*Epitrix
cucumeris* Harris)

Rand and Enlows (1916, 1920) and
Rand and Cash (1920) have shown that
infection does not occur through the
stomata and that wounds involving the
vascular bundles are most effective as
infection courts   These authors have
made extensive studies of the relation
of insects to the disease, and most of
the available information is from their
work   They have shown that the
insects serve not only as agents of dis-
semination and inoculation but that the
adult beetle of *D vittata* (the most
common of the two beetles on cucurbits)
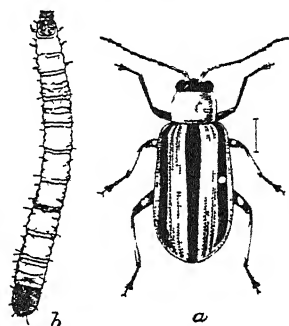
Fig 81 —The striped cu-
cumber beetle (*Diabrotica
vittata* Fabr), the principal
vector of bacterial wilt of
cucurbits   *a,* adult beetle
b,   larva   Approx   5 ×
(*After Chittenden*)

may harbor the pathogen over winter in its body   Primary
infection in the spring always originates from the feeding punc-
tures of such overwintered beetles   Not all beetles harbor the
pathogen   It was recovered experimentally from a relatively
small percentage of the overwintered beetles tested, but only a
small number would be necessary to establish centers of infection
for secondary spread   Confirmatory evidence of this method of
overwintering has been furnished by Doolittle (1921)

The life of the bacterium in the insect body has not been
studied in detail by histological methods, and it is not known
whether any symbiotic relationship exists   However, Rand and
Enlows (1920) have shown that the bacteria pass uninjured
through the intestinal tract of the beetles and may be recovered
from the feces   Rand and Cash (1920) have demonstrated
experimentally that the feces from infective beetles may serve
as effective inoculum only if they are dropped into a fresh feeding

wound   Observations indicate that such contaminated feces may be important as inoculum at night when the plants are covered with dew or in rainy weather

The possible association of the pathogen with the larvae of the beetles has not been investigated adequately   Since the larvae commonly feed on the roots and make wounds in the vascular system, it is entirely possible that they also may be vectors of the disease   When larvae feed on infected plants, they in all probability ingest the pathogen, but the larvae usually do not migrate from plant to plant   The fate of these bacteria in the
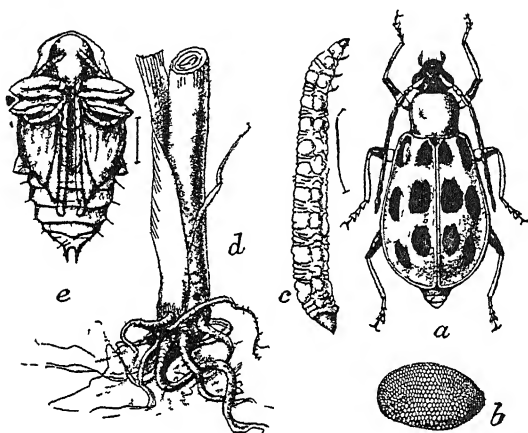
Fig 82 —The spotted cucumber beetle (*Diabrotica duodecimpunctata*), a vector of bacterial wilt of cucurbits   The larva of this insect is also an important vector of the bacterial wilt of corn   *a*, adult, *b*, egg, *c*, larva, *d*, work of larva at base of a corn stalk, *e*, pupa   (*After Chittenden*)

intestinal tract of the larva should be determined   It should be known whether the bacteria survive through the pupal stage and appear in the body of the emerging adult

Bacterial Wilt of Corn (Stewart's Disease) —The bacterial wilt of corn was described in 1897 by Stewart, who had first observed it on Long Island, N Y , in 1895   It is primarily a disease of sweet corn, although field corn, teosinte (*Euchlaena mexicana*), and *Tripsacum dactyloides* are known to be susceptible   Wilt is caused by a yellow, nonmotile bacterium [*Phytomonas stewarti* (Erw Smith) Bergey *et al*]   Ivanoff (1933, 1935) has reported that other bacteria may cause symptoms similar to those caused by this organism   This species is, however, the most prevalent

and the most important   The pathogen is primarily a vascular
parasite although other tissues are often affected   Long, green-
ish-yellow lesions following the veins are formed on the leaves
(Fig 83)   These later turn brown and dry   The entire plant
eventually wilts and may die in any stage of development (Fig
84)   The yellow bacterial exudate that comes from the vascular
bundles when the stalk is cut in cross section is an important
diagnostic symptom (Fig 85)

Wilt is known only in North America and is most prevalent
in the eastern and southern part of the United States   The
disease occured only sporadically in the years following its
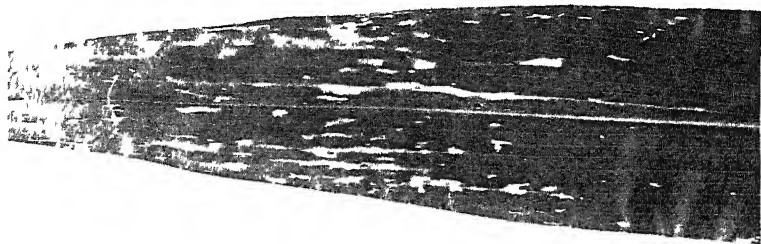
Fig 83 —A corn leaf showing wilt lesions that originated at the feeding
wounds made by the corn flea beetle   Note the tendency of the lesions to follow
the course of the veins   (*After Elliott*)

discovery, but in 1932 and 1933 it became epiphytotic throughout
the southeast section of the corn belt   In these years, the
disease was very destructive, especially on the early varieties of
sweet corn, and numerous reports of 100 per cent losses were
recorded   Renewed interest in the disease has led to the dis-
covery of new and important facts, especially concerning the
relation of insects to its spread and development

The early work of Stewart (1897) and Smith (1914) led
them to believe that the disease was primarily seed-borne,
although infection on aboveground parts was recognized   Natu-
ral internal infection as well as surface contamination of seed
produced on infected plants was demonstrated by Smith (1914),
and it was assumed that the amount of seed infection would
determine the amount of disease in a given crop, although the
possibility of direct infection from infested soil was not over-
looked   Rand and Cash (1921) could find no evidence of infec-

tion from the soil, and similar results were reported in the same
year by Reddy (1921)   Rand and Cash noted also that infected
seed when planted in different regions and at different times
gave widely differing amounts of disease, indicating   some
unknown source of infection

FIG 84 —Young corn plants affected with bacterial wilt   The two center
plants are heavily infected and partly wilted   The plant on the extreme left is
lightly infected, and the one on the right is healthy

The first proof of insect dissemination of the disease was
presented by Rand (1923)   By means of cage experiments, he
demonstrated that the brassy flea beetle (*Chaetocnema pulicaria*
Melsh) was responsible for secondary spread of wilt in mid-
summer (Fig 86)   In 1924, Rand and Cash presented more
data and proved that the toothed flea beetle (*C denticulata* Ill)
also is a vector   In addition, they presented circumstantial
evidence as a basis for the hypothesis that "the early seasonal
incidence of the disease is due largely to the introduction of the

bacterial parasites by insects working at the roots or base of the stems " They concluded that the probabilities were strongly in favor of primary infection being induced by the wounds made by the southern corn rootworm (*Diabrotica duodecimpunctata* Oliv) (Fig 82) A more complete report was published by Rand and Cash in 1933 in which this hypothesis was verified by experimental evidence

The discovery and recognition of the association of flea beetles with bacterial wilt probably explains the unusually severe type of injury often attributed to these insects of corn Forbes (1905) reports the wilting of corn plants attacked by flea beetles in
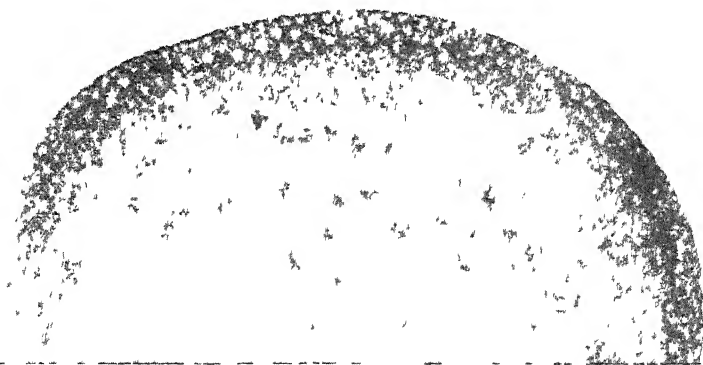
Fig 85—A cross section through a corn stem affected with bacterial wilt showing the bacteria oozing from infected vascular bundles 6 X *(Courtesy of Bureau of Plant Industry, U S Department of Agriculture)*

Illinois in 1891, and Metcalf and Flint (1928) describe flea-beetle injury on corn as follows "Growth is retarded and the leaves wilt even during wet weather " In all probability, bacterial wilt was present on these plants but was not recognized

Ivanoff (1933) showed that, although the pathogenic bacteria were carried in the chalazal tissues of infected seed the embryo was not infected and the seedlings would not become infected from this source unless wounded Infection followed injury of the roots of seedlings by white grubs (*Phyllophaga spp*) and the larvae of the western corn rootworm (*Diabrotica longicornis* Say) and by artificial injury

Elliott and Poos (1934) demonstrated that the pathogen commonly survives the winter in the intestinal tracts of the brassy

flea beetle (*C   pulıcaına* Mclsh)   Oveıwıntered adults caught
ın Apııl were found to have large quantıtıcs of the pathogenıc
bacterıa ın theır ıntestınal tıacts, and when beetles fıom the same
collectıon weıe allowed to feed on hcalthy coın plants ın the
greenhouse, typıcal wılt was pıoduced   Appıoxımately 19 peı
cent of the beetles studıed were found to caıı y the pathogen, but
thıs specıes was the only one of a large numbeı of ınsects tested
that harbored the bacterıa   The hıstologıcal detaıls of the sur-
vıval ın the body of the ınsect have not been repoıted   The
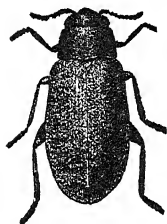
Fıɢ 86 —The corn
flea beetle (*Chaetoc-
nema pulıcaııa*)   Ap-
proʋ 20 ×   Thıs ın-
sect ıs the prıncıpal
ʋector of the bacterıal
wılt of coın   The
bacterıa causıng the
wılt lıve oʋeı wınteı
ın the bodıes of huber-
natıng beetles   (*From
Illınoıs State Natural
Hıstory Survey*)

importance of ınsects ın the epıphytology ot
wılt has been dıscussed ın consıderable detaıl
by Ellıott (1935)

Frutchey (1936) has demonstıated that the
seed-corn maggot [*Hylemyıa cılıcı uı a* (Rond)]
(Fıg 71) also may play an ımpoıtant ıole ın
the development ot the dısease   The laıvae
of thıs ınsect were found ın a laıge numbeı of
dıseased plants ın thc fıeld   When adult flıes
were caged on coın plants, eggs weıe depos-
ıted, and the laıvae attacked the ıoots and
cıown of the plants   Sıxty-seven out of 93
plants, or 72 peı cent, became ınfected wıth
wılt, and eveıy wılted plant showed maggot
ınjury   Only an occasıonal wılted plant was
found ın the controls   Thıs expeıımcnt,
however, does not pıove whetheı the ınsect ıs

a vector or merely an agent of ıngıessıon   The meıe woundıng of
the plants ın the presence of the pathogen would account foı the
observed results   In vıew of the ımpoıtance of thıs ınsect ın the
development of the bacterıal soft rots and ıts known symbıotıc
relatıons wıth bacterıa (Leach 1931b, 1933), ıts ıole ın thc develop-
ment of thıs dısease should be moıe thoıoughly ınvestıgated

Further study of the assocıatıon of all these ınsects wıth the
bacterıa ıs needed   The bacteııa aıe known to lıve foı some tıme
wıthın the body of the adult beetles of the southeın coın root-
woım (*D   duodecımpunctata*), but Rand and Cash (1933) thınk
thıs ınsect ıs of less ımportance ın the spread of mıdsummeı
ınfectıon than the flea beetles   It ıs known that the laıvae make
the wounds necessary foı ınfectıon through the base of the plants,
but theır sıgnıfıcance ın dıssemınatıon of the pathogen ıs not

known   In view of the fact that bacteria are known to survive through pupation in some insects and in some cases are disseminated on or in the eggs, it is of vital importance that these relationships be studied in detail

Stevens (1933, 1934, 1937) has discussed the relation of winter temperatures to the abundance of corn wilt the following summer, pointing out that the disease appears to be worse following mild winters   If it can be shown that there is a direct and consistent relationship between winter temperatures and the prevalence of the disease in the following summer, it would provide a reliable means of predicting epiphytotics and avoiding losses   Since there appears to be no direct influence of winter temperatures on the disease, its indirect influence on the prevalence of insects which harbor the disease over winter, and on which the bacteria depend for ingression, appears to be a probable explanation More complete information however, is necessary before this can be accepted as the true explanation   Support for this theory is found in the observations reported by Elliott (1938) in which the prevalence of the disease in the northeastern states in 1938 was closely correlated with the prevalence of the flea beetle (*C pulicaria*)   In this year, the prevalence of the disease increased rapidly in early summer but decreased strikingly in late summer   The beetles also were abundant until the middle of July but decreased rapidly until very few could be found in late August

Haenseler (1937) made a similar study of the disease based on records from 1910 to 1937 in New Jersey   He confirmed Steven's conclusions in general but expressed the belief that the relationship was not so simple that reliable predictions could be made without further study   He showed there was evidence of a lag period following a severe winter before the full effect is felt   A similar lag period following a mild winter indicated that more than one year was necessary for building up the disease to epiphytotic prevalence   It should also be recalled that insect parasites and other factors may influence the prevalence of the vectors of wilt

Wellhausen (1937) has demonstrated a modification of the virulence of the wilt pathogen as a result of passage through suscepts of differing degrees of resistance the strain becoming less virulent after passage through very susceptible hosts   It

was suggested that this phenomenon might influence the epiphytology of the disease   The introduction of wilt-resistant varieties of sweet corn is contributing much to the practical control of the disease (G M Smith 1933, Ivanoff and Riker 1936), and the variety Golden Cross Bantam and other resistant hybrids are rapidly replacing the more susceptible varieties (Stevens 1937)

Olive Knot —The olive is subject to a bacterial disease causing "knots," or galls, on the branches of the tree (Fig 87)   The

Fig 87 —Olive knot caused by *Phytomonas savastanoi*   *A*, a heavily infected tree, *B*, a single small branch with seven knots   (*After Wilson*)

disease is prevalent in Italy and other countries of southern Europe and has been known in California since 1898 (Wilson 1935)   Olive knot is caused by *Phytomonas savastanoi* (Erw Smith) Bergey *et al*   Infection is known to occur commonly through wounds made by freezing, pruning operations, or other agencies and also through leaf scars (Horne, Parker, and Daines 1912, Wilson 1935)   Rain water appears to be the principal agent of inoculation in California and probably elsewhere, but Petri (1909, 1910) has reported that in Italy the disease is closely associated with the olive fly (*Dacus oleae* Rossi)   He

has described a highly developed symbiotic relationship between
D oleae and certain species of bacteria These bacteria are
constantly found in the intestinal tract of the insect in all stages
of development The bacteria are transmitted internally
through the egg and survive in the puparium Striking anatomi-
cal modifications are found in the insect which ensure perpetua-
tion of the bacteria through successive generations Among
the bacteria frequently occurring as a symbiote is a nonpatho-
genic species (*Ascobacterium luteum*) but according to Petri
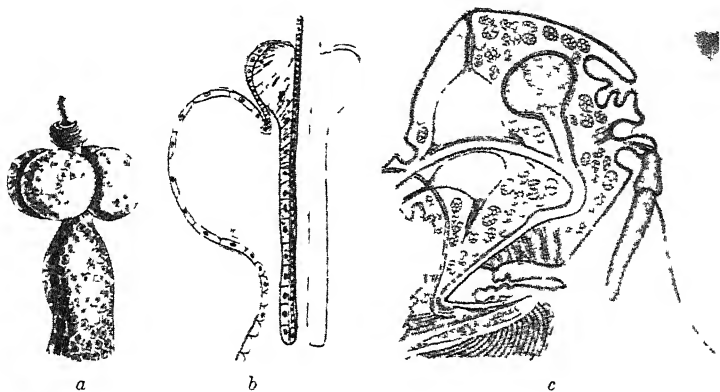
Fig 88 —*a*, the anterior portion of the mid-intestine of the larva of *Dacus
oleae*, in perspective showing the caeca filled with bacteria *b* the same as seen
in section *c* a longitudinal section of the head of an imago of *Dacus oleae* showing
the bulbous diverticulum off the esophagus During metamorphosis, the bac-
teria from the intestinal tract accumulate in this organ from which the entire
intestinal tract is later recontaminated (*After Petri*)

the olive-knot pathogen also is usually present Although it is
difficult to isolate in pure culture directly from the insect its
presence can be demonstrated by inoculating olive branches
with the mixed cultures The histological aspects of this symbi-
otic association have been verified by Stammer (1929) who also
has described in other species of Trypetidae a series of symbiotic
relationships with anatomical adaptations of various degrees of
complexity

Because of the highly developed symbiotic relationship pic-
tured here, the association will be described in some detail
The principal features have been graphically illustrated by Petri
as shown in Figs 88, 89, and 90 Petri has demonstrated that

the intestinal tract of the fly is constantly contaminated with the
bacteria, some of which pass out uninjured in the feces   In the
female fly, the anal tract and the vagina unite at their posterior
end to form a common opening to the exterior (Figs 89 and 90)
In the wall of the anal tract near the point of union, there are a
number of saclike evaginations that open into the lumen   These
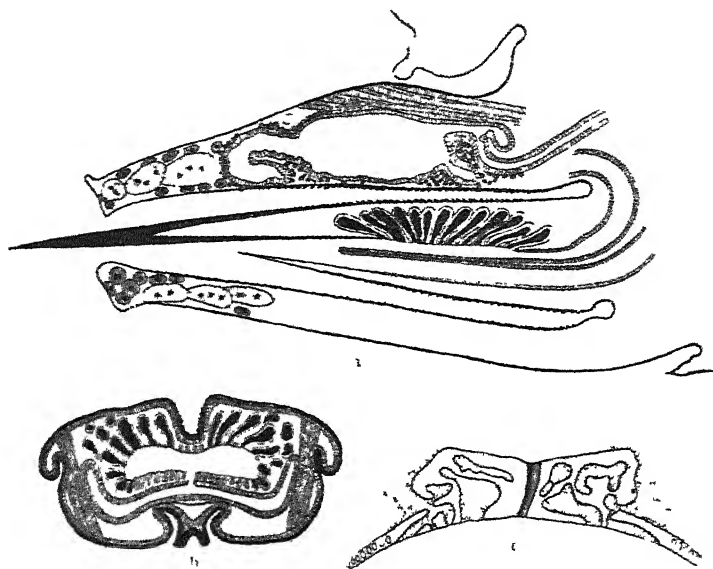
Fig 89 —The ovipositor of *Dacus oleae*, a vector of olive knot showing the
anatomical adaptation for congenital transmission of bacteria   *a*, a longitudinal
section of the ovipositor showing the common opening of the vagina and the anal
tract and the saclike evaginations of the anal tract in which the bacteria are
found *b* a cross section of the ovipositor showing the longitudinal slit connecting
the anal tract and the oviduct the eggs on passing out press against the pockets
and become smeared with bacteria *c*, a section through the micropyle of an egg
through which the bacteria enter the egg to infect the embryo   (*After Petri*)

are always filled with bacteria   Immediately opposite the open-
ing of the evaginations there is a longitudinal slit in the mem-
brane, separating the anal tract from the oviduct   When the
eggs pass along the vagina this slit is spread open so that the
surface of the egg is pressed against the openings of the bacteria-
filled evaginations   In this way the bacteria are smeared over
the surface of the egg

Petri has shown that the bacteria find their way through the
micropylar openings into the interior of the eggs and into the
body of the developing embryos (Fig 89c)   The larvae are,
therefore   always internally contaminated with the bacteria
before they hatch from the egg   Near the fore part of the mid-
intestine of the larva are four spherical caeca that harbor the
bacteria (Figs 88a and b) which may be found distributed through-
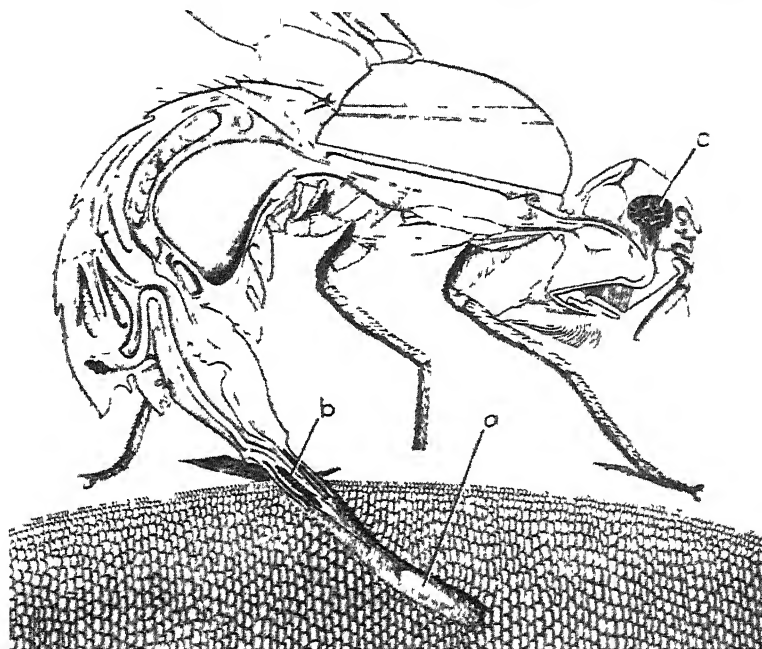
FIG 90 — A diagrammatic sketch showing how the eggs of *Dacus cvae* are
deposited and how the tissues of the plant are inoculated with bacteria   *a*   *c*
egg, *b*, saclike evaginations of the anal tract filled with bacteria *c* diverticulum
of esophagus filled with bacteria   (*After Petri*)

out the contents of the intestinal tract   When the larva pupates
the bacteria decrease in number but do not entirely disappear,
for when the fly emerges from the puparium, it is always inter-
nally contaminated   A peculiar spherical diverticulum is devel-
oped off the esophagus just in front of the brain of the pupa
(Fig 88c)   This diverticulum soon becomes filled with the
bacteria   Shortly after the imago emerges from the puparium,
the entire intestinal tract, including the anal sacs becomes
contaminated from this reservoir   By this specialized adapta-

tion, the perpetuation of the symbiotic bacteria is ensured
The bacteria are inserted into the wounds made in oviposition
(Fig 90), and according to Petri such wounds are infection courts
for much of the olive knot in Italy   In California, where this
insect does not occur, the bacteria depend chiefly on wind-blown
rain for spreading from tree to tree, and the rate of spread from a
center of infection is relatively slow (Wilson 1935)   It is entirely
probable that the spread would be more rapid if the insect were
present

Stammer (1929) has shown by histological studies that many
species of Trypetidae harbor symbiotic bacteria   It has been
shown (Allen and Riker 1932) that the Trypetid apple maggot
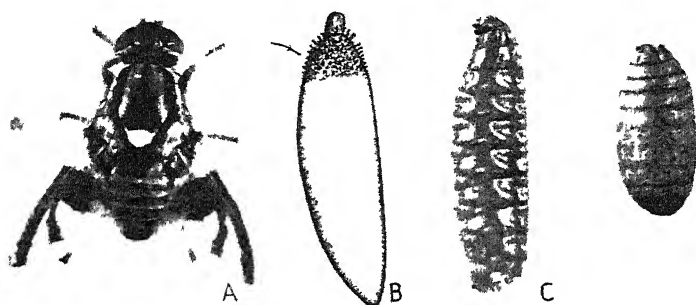
Fig 91 —The apple maggot fly (*Rhogoletis pomonella*)   *A*, adult female, *B*, egg,
C, larva, *D*, puparium   (*After Allen, Pinckard, and Riker*)

(*Rhagoletis pomonella* Walsh) is a regular vector of a bacterial rot
of apples and that there is a close symbiotic association between
the insect and the pathogenic bacteria   Whenever a representa-
tive of this group of insects is found associated with a bacterial
disease, it should be considered as a potential vector

Bacterial Rot of Apples and the Apple Maggot —Although
many people have observed that a decay of apples often followed
infestation by the apple maggot (*Rhagoletis pomonella* Walsh)
(Fig 91) no particular significance was attached to the associa-
tion   It was generally assumed that the breakdown of the
tissue (Fig 92) was due to the activity of the maggots alone or to
chance entrance of pathogens through the wounds made by the
insects   Allen (1931) reported that the decay associated with
maggot injury was caused by bacteria and suggested that they
were disseminated by the adult flies   Allen and Riker (1932)

published a more complete account of the decay, described the
pathogen, and named it *Phytomonas melophthora*   In 1934,
Allen Pinckard, and Riker described in considerable detail the
association of the bacteria with the various stages of the life cycle
of the apple maggot

The female fly deposits her eggs in the apple fruit by making
a puncture through the epidermis with her sharp pointed ovi-
positor (Fig 93)   The eggs hatch in 2 to 9 days, the larvae
tunnel through the flesh of the apple and aided by the bacteria
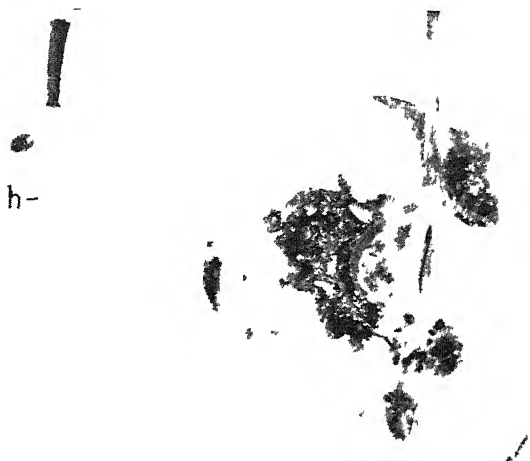
Fig 92 —Apples showing decay associated with larval tunnels o the apple
maggot   The decay is caused by *Phytomonas melophthora* and is transmitted
exclusively by the apple maggot   A surface view showing decay originating at
oviposition punctures (*h*), *B*, section showing internal decay and larval activity
(*After Allen and Riker, and Allen, Pinckard, and Riker*)

with which they inoculate the apple, soon render the fruit worth-
less   The length of the larval period varies from 2 or 3 weeks to
several months   The rate of development is slower in green
apples than in ripe ones   When the maggots are mature, they
leave the apples and enter the ground to pupate   The insect
lives over winter in the pupal stage and emerges the following
summer

The bacteria are found associated, externally and internally
with both male and female flies   They also were isolated in
about 50 per cent of the trials from oviposition punctures and
equally as often from the surface of eggs removed from apple

tissue   Two larvae that hatched from surface-sterilized eggs were sterile, a fact indicating that the bacteria do not occur inside the egg but that they have ample opportunity of becoming contaminated by the bacteria borne on the surface of the eggs

The tissue of green apples appears to be resistant to the bacteria, which cause very little decay before the fruit begins to ripen
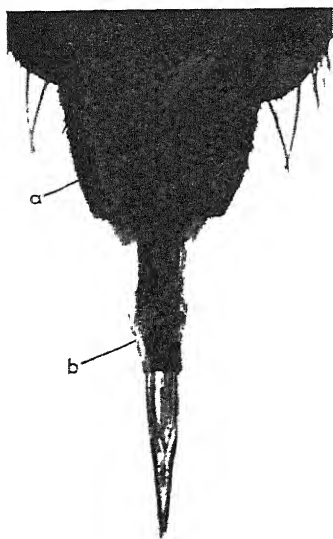
FIG 93 —The ovipositor of the apple maggot fly partly extended *a* end of abdomen, *b* tip of ovipositor   By means of this sharp pointed structure the fly punctures the apple tissue and inserts an egg, at the same time inoculating the apple tissue with pathogenic bacteria carried on the surface of the egg   23 ×   (*After Allen, Pinckard, and Riker*)
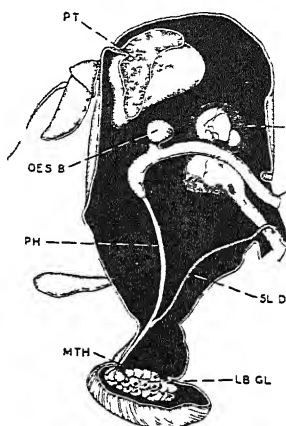
FIG 94 —A section through the head of an apple maggot showing, among other structures the ' oesophageal bulb ' (*OES B*)   Its function is not known, although a similar structure in the olive fly (*Dacus oleae*) harbors symbiotic bacteria during metamorphosis   *PT* ptilinum, *BR* brain, *OES*, oesophagus, *PH* pharynx *SLD*, salivary duct, *MTH*, mouth, *LBGL*, labial gland (*After Dean*)

The development of the larvae may be dependent upon the bacterial growth, for the maggots appear to prefer the decayed tissue   Two sterile maggots failed to live in apple tissue, while maggots from non-sterilized eggs grew and pupated normally No further studies on the nutritional significance of the bacteria have been reported

Bacteria were not isolated from the interior of the puparia although they were abundant on its surface   It was mentioned that considerable difficulty in isolation of the pathogen was

caused by contaminating bacteria   In view of the frequency
of the survival of bacteria in the puparia of other Diptera (Stammer 1929, Leach 1933, Aik and Thomas 1936), it would appear
that this aspect of the association needs further investigation

No histological studies were reported by Allen, Pinckard, and
Riker, but Dean (1933 1935) has reported on certain phases of
the morphology and anatomy of the apple maggot   There are
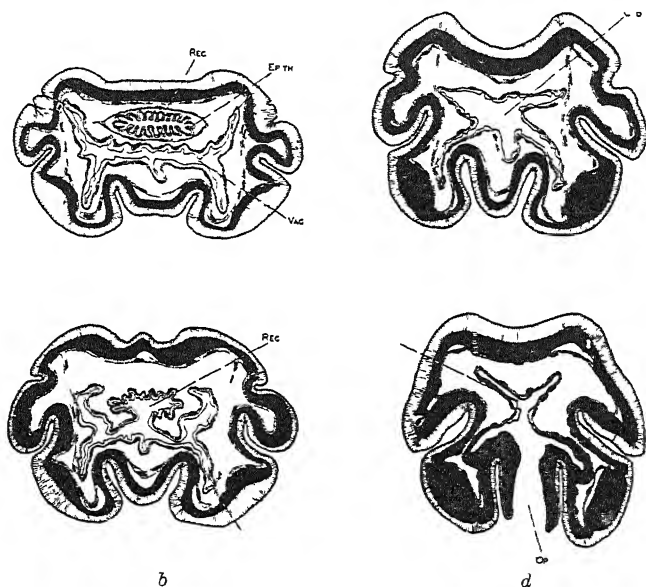
Fig 95 —Cross section of the ovipositor of the apple maggot fly at four points
near the posterior end, showing the union of rectum and vagina   *a*, the most
anterior section showing the rectum (*REC*) and vagina (*VAG*) separate   Note the
numerous deverticula in the epithelium (*EPITH*) of the rectum, *b*, a more posterior
section showing the rectum and vagina beginning to unite, *c*, the rectum and
vagina completely united into a common cloacal passage (*CLO*), *d*, the external
opening of the cloaca (*OP*)   Approx 200×   (*After Dean*)

certain points of similarity in the anatomy of this insect with that
of *Dacus oleae* which are significant   A peculiar evagination of
the esophagus similar in all respects to that described in *D oleae*
by Petri (1909, 1910) was reported by Dean (Fig 94) who
apparently was not familiar with the work of Petri and made no
attempt to determine the function of this structure which he
called the " esophageal bulb "   It should be determined whether
or not the bacteria that survive through metamorphosis occupy
this organ as they do in *D oleae*

There also is a striking similarity in structure of the ovipositor and anal tract of the two insects   Dean reported that the rectum and vagina of the apple-maggot fly unite to form a common passage   His illustrations show the same type of evaginations of the anal tract to form numerous sacs similar to those described with respect to *D oleae* by Petri although no special mention is made of them (Fig 95)   A closer study of these structures with particular reference to their association with symbiotic bacteria should be made   In all probability it will be found that the pathogenic bacteria are transmitted on or in the egg as in *D oleae*

Gummosis of Sugar Cane—One of the more destructive diseases of sugar cane is that known as "gumming" or "gummosis "   It is caused by a bacterium [*Phytomonas vascularum* (Cobb) Bergey *et al*] that develops primarily as a vascular parasite causing copius exudates of a sticky gum, a characteristic that is responsible for the name of the disease   The disease has been known since 1869 but was first adequately described by Cobb (1893, 1895) who showed that it was caused by a bacterium, which he named *Bacillus vascularum*   The pathogen was more completely described and its pathogenicity verified by R G Smith (1902) and by E F Smith (1904)   The most thorough study of the disease and its method of spread under field conditions has been made by North (1935)

Gummosis of sugar cane is strictly confined to the sugarcane plant   No other plant is known to be affected in nature, although there is some evidence that the disease may have originated in South America where sugar cane is not indigenous If this is true it would be necessary to assume its pathogenicity on some plant native to South America

Affected plants are dwarfed and long yellow streaks appear on the leaves   The streaks later wither and become brown, the leaves dying from the tip toward the base   A pronounced yellow slime that forms in the vascular bundles is the best diagnostic symptom   The infection spreads from the vascular bundles into the neighboring cortex and in wet weather a yellowish gummy exudate forms on the surface of affected tissue

Gummosis is transmitted readily by planting infected sets, and, as sugar cane is commonly propagated in this way, this method of transmission is very important   It is the chief method of introducing the disease into new areas and has been responsible

for most of the long-distance spread   The disease also may be transmitted by the cutting knife when canes are being cut for planting

Local secondary spread in the field is effected primarily by wind and rain as demonstrated by North   Gum filled with the pathogenic bacteria, oozes from affected leaves when they are wet   Rain washes the bacteria from the leaves and scatters it to other leaves which are at the same time being injured by the effects of the wind   Infection occurs most commonly through minute wounds made by the serrate edges of one leaf scratching the surface of another leaf

North (1935) made a thorough study of insect transmission of gummosis under field conditions   In an extensive series of cage experiments, only negative evidence was obtained with numerous species of insect that commonly feed on sugar-cane leaves, including aphids leaf hoppers, plant bugs and beetles   However, many species of fly were observed actively feeding on the gummy exudate, especially in wet weather following a rain   It was demonstrated by a series of caging experiments that flies were effective vectors   The flies take shelter in the sugar-cane fields during the rainstorms, and when the storms are over they are attracted to the sap oozing from the fresh wounds   They ingest contaminated gum from infected plants and then feed on exudate from fresh wounds in healthy plants and in this way transmit the disease   It was also demonstrated that the bacteria survive for some time in the intestinal tract of the flies and that the flies may transmit the pathogen for relatively long distances as compared to the local dissemination by wind-blown rain   The importance of transmission by flies is based primarily on relatively long-distance dissemination that gives rise to isolated centers of infection and secondarily on local dissemination as a supplement to dissemination by wind and rain

Control of gummosis depends largely upon the selection of healthy canes for planting, the use of general sanitary practices and the development and planting of resistant varieties   Some progress has been made in the development of resistant varieties, and this method offers the most promise for the other methods are effective only to a limited extent

A Bacterial Disease of Willows and the Willow Borer — Lindeijer (1932) has described a disease of willows in Holland

caused by a species of bacteria which she listed as a new
species (*Pseudomonas salic
perda*), [*Phytomonas saliciperda* (Lind-
eijer) Hauduroy *et al*] The willow borer, or snout beetle
(*Cryptorhynchus lapathi* L), is reported as a vector of the disease

The disease causes a wilt of the branches followed by early
defoliation and death of the affected limbs, either the first or
second year after infection (Fig 96a) The pathogen is a vascu-
lar parasite It is a capsulate organism that clogs the vessels
and cuts off the transpiration stream The terminal portions of
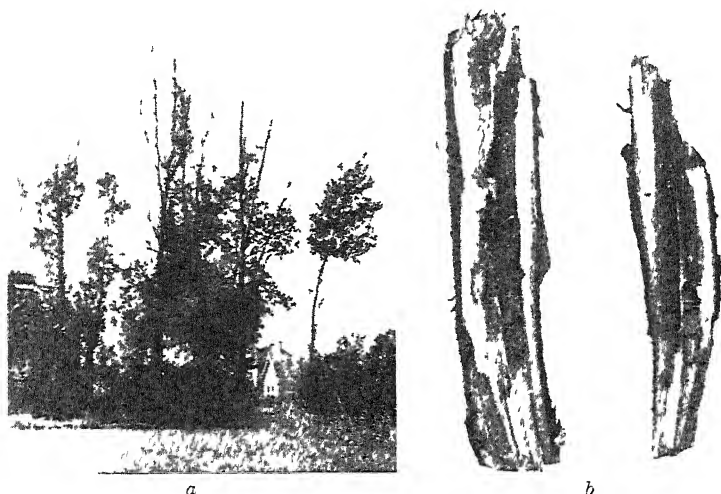
Fig 96 —Bacteriosis of willow   *a*, a group of willow trees killed by bac-
teriosis, *b* two twigs with burrows made by *Cryptorrhyncus lapathi*, the vector of
the disease   (*After Lindeijer*)

the branches dry out, whereas the lower parts become water-
logged Infection can occur only through fresh wounds that
penetrate the bark and reach vessels of the wood

The necessary wounds are usually furnished by the feeding
and breeding activities of the willow borer This insect feeds
upon the bark and the outer layers of the wood Observations
showed that natural infections most frequently originated at the
wounds made by the insect The borer feeds readily upon
infected branches and in so doing becomes contaminated with
the bacteria (Fig 96b) The disease was experimentally pro-
duced by allowing insects, both naturally and artificially con-

taminated with the bacteria, to feed upon willow twigs   The bacteria also were isolated from the esophagus of beetles that had fed upon infected branches

The borer also breeds in willow twigs, but eggs deposited in infested wood rarely hatch because of the excessive moisture It is concluded, therefore, that the vector does not as a rule become contaminated from breeding in infested wood although it may be contaminated from walking over the bacterial ooze that is often exuded from cracks in affected branches

Bacterial Wilt of Solanaceae —Potatoes, tobacco tomatoes peppers, and other related plants are severely affected with a bacterial wilt caused by *Phytomonas solanacearum* (Erw Smith) Bergey *et al*   Numerous plants in families other than the Solanaceae also are affected to some extent   It is prevalent throughout the southern part of the United States and has been reported from Europe and several places in the tropical regions of the world   It appears to be favored by warm weather and is most destructive in warmer regions

The first symptom of the disease is a sudden wilting of the leaves on a single branch or on the entire plant   This is soon followed by a shriveling of the stems and eventually the death of the plant   The bacteria are found first in the vascular bundles which become brown throughout almost the entire plant, but eventually they enter the parenchyma cells of the cortex and pith and destroy them as well   The bacteria spread through the vascular bundles of the stolons until they reach the tubers where the vascular ring is first destroyed, and the decay of the storage tissues soon follows   When affected stem or tubers are cut in cross section, the bacteria ooze out in a brownish yellow slime

From a study of the literature on this disease it is evident that many details of the methods of infection and spread in the field are not known definitely   Smith (1896) succeeded in transmitting the disease in the greenhouse by means of potato beetles (*Leptinotarsa decimlineata* Say)   Potato beetles, having previously fed on infected plants, were placed for several hours on four healthy plants under large bell jars after which they were removed   Within 7 to 9 days, all the inoculated plants developed typical symptoms, while the controls remained free   From these experiments, Smith generalized as follows

These experiments with the Colorado potato beetle seem to fully warrant the conclusion that insect enemies are largely responsible for the spread of the disease   Given one diseased vine in a field and plenty of insects to feed upon it, the transmission of this disease to all parts of the field and thence to the whole neighborhood, is only a question of weeks

Just what insects are most instrumental in disseminating this parasite in any particular locality can be determined only after a prolonged and careful study of the disease in the field   No experiments have been made with other insects, but it is likely that flea beetles, blister beetles, chrysomelids, and many other leaf-eating insects may act as carriers of the disease

These general conclusions have been repeated by subsequent writers, but the "prolonged and careful study of the disease in the field ' seems never to have been made

Although Smith (1896) concluded that most of the infections probably occur aboveground as the result of insect injuries, his views were modified later (1914), and much circumstantial evidence has been presented by various workers, indicating that in nature infections occur most commonly on the underground parts The recent work of Eddins (1936), in which effective control of the disease on potatoes was obtained by adding sulphur to the soil, lends weight to the latter conclusion

The available evidence indicates that infection occurs only through wounds   At least, it has never been demonstrated that infection can occur in the absence of wounds   If wounds on the underground parts are necessary for infection it is very probable that insects are involved   A thorough study of the soil insects that commonly affect the roots of susceptible plants would probably throw some light on the question   Smith (1914) has suggested a possible relationship with the root-knot nematode but no experimental study of the relationship has been reported

Bacteriosis of Prickly-pear Plants —Johnson and Hitchcock (1923) have described a bacterial disease of prickly pear (*Opuntia spp*) which is transmitted by a number of insects that feed upon these plants   The disease was discovered in Florida and later introduced into Australia where it was studied as a possible aid in the control of prickly pears

The disease is caused by a species of bacteria described and named by Johnson and Hitchcock as *Bacillus cacticidus*, [*Erwinia*

cacticida (Johnson and Hitchcock) Hauduroy *et al*] The bacteria cause is rapidly developing soft rot of affected tissues The decay is limited almost entirely to the succulent parenchyma tissues, the bacteria failing to spread through the vascular bundles A distinct purplish discoloration is characteristic of the affected tissues in the earlier stages of decay The parenchyma is ultimately reduced to a brown, slimy, fetid liquid that dries out leaving only the cuticle and vascular strands

Inoculation experiments with the pathogen revealed a high degree of specificity for the various species of *Opuntia* The most commonly grown fruits, vegetables, and forage crops are not susceptible to the disease The pathogen is an actively motile, Gram-negative, aerobic and facultative anaerobic short rod In general character, it resembles very closely the omnivorous *Erwinia carotovora* but is more limited in its host range

The pathogen will not infect through the stomata and is in all probability, a strict wound parasite It was demonstrated experimentally that the larvae (caterpillars) of several insect pests of the cactus, including *Melitara prodenialis, Olyca junctolineella,* and *Mimorista flavidissimalis* are effective vectors of the disease, and it was predicted that *Cactoblastis cactorum* and *C bucyrus* would also prove to be effective vectors The larvae of the longicorn beetles (*Moneilema spp*) and several members of the Drosophilidae also were shown to be capable of transmitting the disease

The insect vectors of this disease are important not only in transmitting the disease from plant to plant but also in transmitting infection from one segment to another of the same plant The infection will not spread unaided from one segment to another, for the bacteria affect only the parenchyma tissues and are unable to invade the lignified vascular tissues Without the aid of the insect vectors, the disease, at most would produce only local lesions on isolated leaf segments

It is not known to what extent this bacterial disease has contributed to the destruction of prickly pears in Australia (see Figs 5 and 6), but Dodd (1936), in discussing the manner of destruction of prickly pears by the introduced insect (*C cactorum*) stated

The larvae of *Cactoblastis* devour the whole of the cladodes except the vascular bundles and the thin papery cuticle, and the injured segments

dry out   More often, however, the tunneling of the larvae sets up conditions favorable for plant diseases, bacterial in the more terminal growth, fungus infections in the thicker lower portions, in consequence, destruction is hastened

Bacterial Gall of Douglas Fir and Chermes Cooleyi —Hansen and Smith (1937) have described, on Douglas fir in California, a bacterial disease that they believe is insect-transmitted   The disease causes rough globular galls on the young twigs and branches (Fig 97)   The gall is composed of hypertrophied
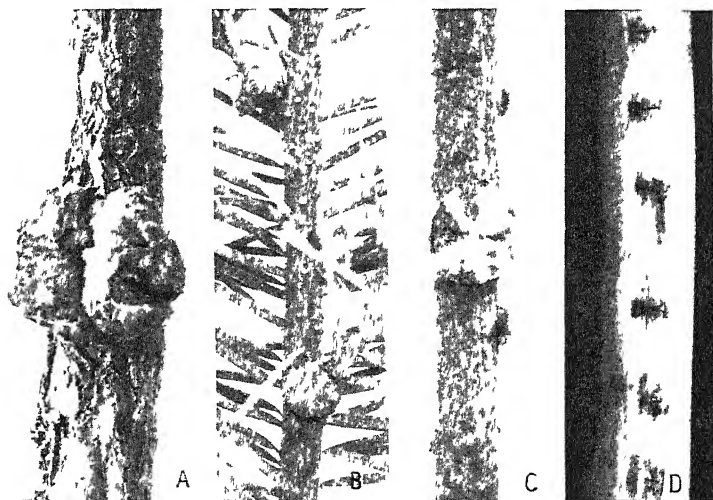
FIG 97 —Bacterial gall of Douglas fir   *A*, a naturally occurring gall *B* and *C*, galls produced by artificial inoculation, *D* a fir twig with bark removed to show feeding wounds made by *Chermes cooleyi* through which infections occur in nature   (*After Hansen and Smith*)

tissue involving both cortex and stele   The galls have their origin always within the tissues of the stele, and artificial inoculations demonstrated that infection occurs only when the pathogenic bacteria (*Bacterium pseudotsugae* Hansen and Smith) are placed in actual contact with the xylem elements

The dependence of infection upon deep wounds suggested transmission by an insect vector of some sort   Two insects were present in sufficient abundance to invite suspicion   One of these, the orchard cicada (*Platypedia areolata* Uhler), oviposits in the twigs and thus causes deep wounds that reach the xylem elements   Over two hundred oviposition wounds were examined, but galls

were never associated with them. The other possible vector, Cooley's Chermes (*Chermes cooleyi* Gill), is a sucking insect belonging to the family Chermidae. It feeds on the small twigs and makes deep wounds extending into the wood. This insect was observed feeding upon fresh galls, and galls have been found arising from feeding punctures of the insect. Thus strong circumstantial evidence points to this insect as the vector of the disease. No other means of transmission in nature is known.

Black Rot of Crucifers —As early as 1897, E. F. Smith reported experimental transmission of black rot of crucifers [*Phytomonas campestris* (Pammel) Bergey *et al*] by slugs (*Agriolimax agrestis* L.) and the cabbage worm (*Plusia brassicae*). Brenner in 1904 confirmed Smith's experiments with slugs and added an unnamed species of aphid as a vector. These experiments were all based on greenhouse work, and no one has shown that the vectors are of any significance in the development of the disease in nature.

In 1924, Clayton reported experiments in which caged cauliflower plants escaped infection while control plants not protected by cages were heavily infected. This led him to conclude that insects were important vectors in the field. Later experiments (1929), however, failed to support this conclusion. The evidence obtained later led to the belief that the cages prevented spread by wind-blown rain and by contact in cultivation, ways in which he concluded the disease was most frequently spread. Other workers have suggested various insects as possible vectors but have presented little or no experimental data. Until more conclusive evidence is available, it must be assumed that in nature insects are of little significance as vectors of black rot.

Angular Leaf Spot of Tobacco and the Southern Tobacco Worm —Johnson (1934) described an association of the lesions of angular leaf spot [*Phytomonas angulata* (Fromme and Murray) Bergey *et al*] with injuries made in the leaf surface by the tobacco worm in crawling over the leaf. The prolegs of the tobacco worm are equipped with semicircular hooks and are used for clinging to and moving over the surface of the leaf. These hooks make very small punctures in the leaf that serve as infection courts. The prolegs of the worms doubtless are contaminated with the bacteria from leaf-spot lesions. The insect is more effective as an agent of inoculation when the leaves are moist and is responsible for dissemination for very short distances only.

Bean Bacteriosis and Thrips —Buchanan (1932) has shown that *Heliothrips femoralis* Reut may transmit a bacteriosis (halo blight) of beans (*Phytomonas medicaginis* var *phaseolicola* Burkholder) in the greenhouse   The thrips were observed feeding on plants that had not been inoculated with the bacteria   The bacterial lesions were always associated with the feeding wounds of the insects   When thrips were transferred from infected plants to healthy plants, similar lesions were developed about their feeding wounds, while no lesions developed when the thrips were taken from healthy plants   The transmission appears to be incidental and entirely mechanical   The insect probably is of little importance as a vector of the disease under field conditions

Blade Blight of Oats (Halo Blight) —Manns, in 1909, reported experimental evidence showing that aphids were vectors of a bacterial disease of oats which he called "blade blight "   It is probable that this disease is the same as halo blight caused by *Phytomonas coronofaciens* (Elliot) Bergey *et al* (Elliot 1920) Aphids, taken from affected plants and transferred to healthy ones in cages, effectively induced the disease after 10 to 12 days, but when the insects were taken from healthy plants no disease developed   Since Elliot has shown that infection may result from stomatal penetration and that aphids are not necessary for infection, it is probable that these insects play only a minor part in the spread and development of the disease   However, it would be well to study the disease further with particular reference to the role of insects in its transmission

Gardenia Bud Drop —Wilson (1927) has described a bud drop of gardenias said to be caused by an unnamed species of *Erwinia* Infection occurs through the extrafloral nectaries   Observations in greenhouses and experiments in the laboratory demonstrated that the bacteria were disseminated by ants and mealy bugs which commonly feed on the extrafloral nectar

The Spot Disease of Cauliflower and the Red-bordered Stinkbug —Goldsworthy (1926) in a study of the spot disease of cauliflower [*Phytomonas maculicola* (McCulloch) Bergey *et al*] isolated the pathogen from the soil and also from the extremities of the red-bordered stinkbug (*Europthalmus convivus*)   He concluded that the insect was a common agent of dissemination although no experimental proof was given

Bacteria Associated with Aphids and a Gall on Witch Hazel —
Lutz and Brown (1928) have described a species of bacterium
commonly associated with the aphid (*Hamamelistes spinosus*)
and a spiny, hollow bud gall on witch hazel   They suspect that
the bacteria may be the actual cause of the gall but were unable
to prove it by artificial inoculation of witch-hazel buds with
the bacteria

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CHAPTER VII

INSECTS AND FUNGUS DISEASES

Fungi are responsible for more plant diseases than any other group of microorganisms   The great diversity in their morphology, physiology, and life history makes them a very versatile group of plant pathogens   The spores, which constitute the principal inoculum of the pathogenic fungi, are extremely varied and are adapted to many different methods of dissemination   Although wind is the most common agent of dissemination of fungus spores, some pathogenic fungi are almost entirely dependent upon insects, not only for spore dissemination but also for inoculation and ingression

Unlike the bacteria, some species of fungi are able to gain entrance to plant tissues by direct penetration of the epidermal cells   Others depend upon stomata and other natural openings for ingression, but there are some that are completely dependent upon wounds, many of which are made by insects   The adaptive relationships between insects and fungus plants pathogens are as numerous and complicated as those between insects and bacteria

Ergot of Cereals and Grasses —Ergot is a fungus disease attacking many species of cereals and grasses   Of the cultivated cereals, rye is the most severely affected   The disease affects primarily the floral organs which often may be so severely injured that the floret is sterile   More frequently, the kernels are replaced by the large, dark-colored sclerotia of the pathogen   The disease is important not only because of the reduction in crop yield but also because of the harmful effect of the sclerotia when eaten by man or animal   The toxic substances in the ergot fungus have certain medicinal properties and are extracted and used as drugs

The fungus [*Claviceps purpurea* (Fr) Tul] survives the winter in the soil as sclerotia   In late spring, the sclerotia germinate by sending up several stromata, each consisting of a light-colored stalk surmounted by a reddish spherical head (Fig 98)

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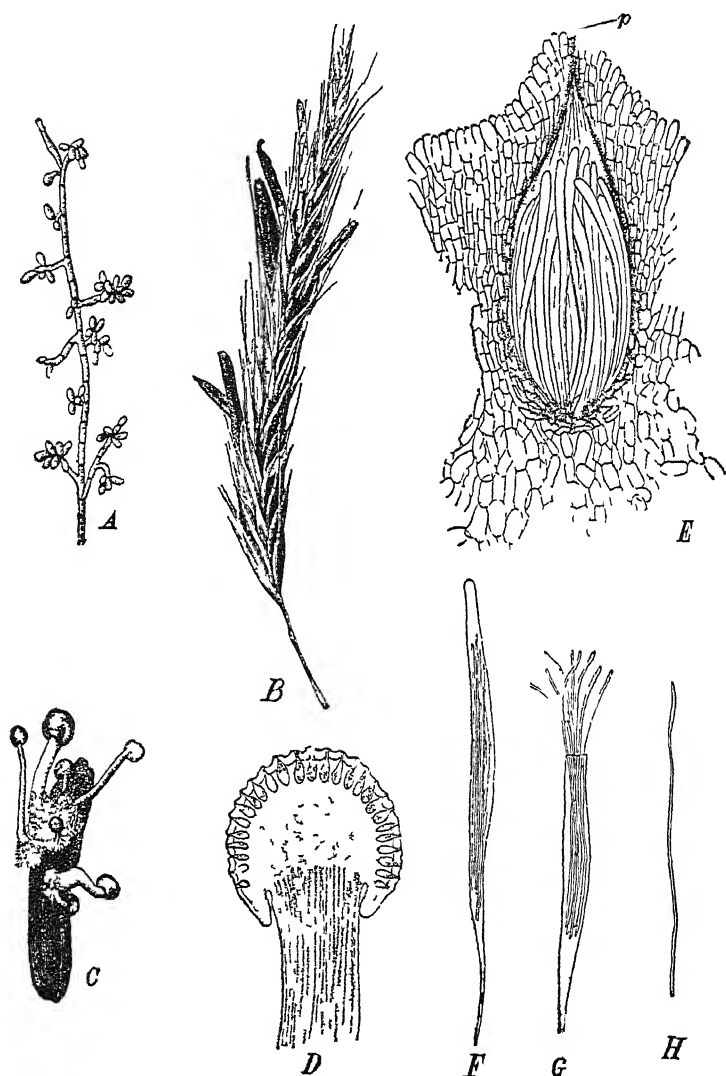
FIG 98 —Ergot of rye (*Claviceps* purpurea)   *A*, conidia (these are born in drops of a sugary solution on the surface of the young sclerotia), *B* mature sclerotia on head of rye, *C*, a germinating sclerotium with a number of perithecial stromata, *D*, an enlarged section through a perithecial stroma showing the perithecia embedded near the surface, *E* section through a single perithecium, *F*, a single ascus *G*, a ruptured ascus with extruding ascospore, *H*, a single ascospore   (*A and B after Strassburger, C-H after Tulasne*)

Embedded under the surface of the heads are large numbers of flask-shaped cavities opening to the outside through small holes marked by minute papillae These cavities are the perithecia in which the ascospores are borne The ascospores are responsible for primary infection

There has been some difference of opinion concerning the manner in which the ascospores are disseminated to the grass flowers where infection occurs Stager (1903) concluded from observations and experiments that the ascospores slowly exude from the perithecia, accumulate on the slimy surface of the stromatic head, and are disseminated by flies Other workers (Wilson 1875, Falck 1911) have shown that the ascospores are often forcibly ejected from the asci, being projected into the air for a distance of 2 to 8 centimeters, after which they are disseminated further by convection currents and wind

Because wind dissemination of ascospores has been demonstrated, it is often stated that insects are of no importance in distributing the ascospores of ergot Such a definite statement does not seem to be justified, for there have been no careful experiments dealing with the subject As early as 1875, Wilson pointed out that, although some of the ascospores are forcibly ejected into the air, others later are gradually exuded from the perithecia where they collect on the surface of the stroma in a sticky liquid If insects are attracted to the stroma as reported by Stager (1910) and if these insects are the same as those which visit the blossoms of rye and other grasses, they would be very effective agents of inoculation Furthermore, it has been shown (Engelke 1901) that the ejection of the ascospores may occur very suddenly in response to a slight touch of the stromatic head An insect alighting upon the stromatic head would provide the necessary stimulus and as a result would become contaminated with the ejected spores

According to Rolfs, as reported by Stevens and Hall (1910), a related fungus (*Claviceps paspali*) is disseminated by beetles of the family *Carabidae* The beetles visit the spore-covered stromata where they become contaminated with spores, then crawl up the grass stems to the inflorescence, and inoculate the young ovaries It is evident from the work of Falck (1911) and others that wind dissemination of ascospores occurs quite commonly, and this may be the usual method, but the possibility

of extensive insect dissemination is not excluded   A more thorough study of ascospore dissemination is needed

Following infection, the ergot fungus permeates the tissues of the ovary, later replacing it with sclerotial tissue   In the early stages of infection, the surface of the developing sclerotium is covered with numerous convolutions on which are borne large quantities of small subspherical conidia (Fig 98)   These spores, measuring from 0 7 to 3 5 microns in diameter, are borne in
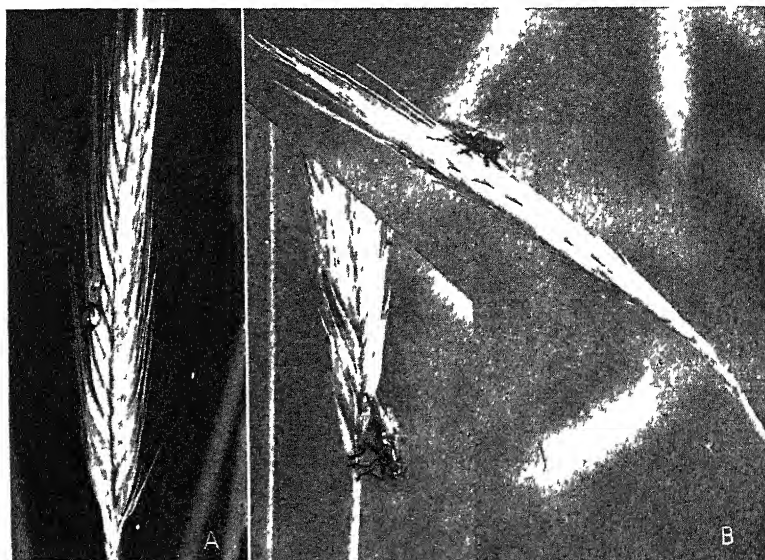
Fig 99 —A, a head of rye showing sugary exudate containing conidia of the ergot fungus, B, flies feeding upon ergot-infected heads of rye

droplets of a sugary solution often called "honeydew"   When disseminated to other flowers, the conidia are responsible for secondary infection

It is generally conceded that insects are the most common agents of disseminating these secondary spores   The conidia, unlike the ascospores, are not forcibly ejected, and being borne in a sticky liquid they are subject to wind dissemination only as the wind may blow one plant's head against another   Moreover, it is a matter of common observation that insects visit the affected florets and feed upon the sugary fluid containing the spores (Fig 99)   The fungus at this stage of development has a dis-

tinctive carrionlike odor that seems to attract insects, especially flies

Atanasoff (1920) states that as early as 1847 Leunis observed the insects visiting the infected florets and suspected that they were disseminating the spores   Mercier (1911), however, was the first to investigate the subject carefully   He showed that a fungus gnat (*Sciara thomae* L) actively disseminated the spores both externally and internally   He showed that the spores were passed through the intestinal tract of the insect without losing their viability   The habit of flies of regurgitating the contents of the crop when feeding would appear to make them particularly effective as vectors

Atanasoff (1920) lists more than 40 different insects that have been observed feeding upon the sugary secretion of ergot Many of these feed not only on the honeydew containing the spores but also on the pollen of healthy flowers, a fact of considerable significance from the standpoint of inoculation efficiency Those insects which regularly visit healthy heads as well as diseased ones would obviously be more effective vectors than those which limit their visits to diseased heads   Despite the large amount of convincing observational evidence of insect dissemination of ergot, relatively little experimental work has been done on the subject, and there are many obscure points that need further study

Bark Beetles and Blue Stain of Coniferous Trees —The sapwood of many species of coniferous trees is attacked by fungi that stain it dark blue, although the fungi do not decay the wood, the discoloration greatly reduces its market value (Fig 100) Although blue stain is most frequently found in felled timber, it is not uncommon in living trees that have been weakened by drought, fire, or some other adverse factor   When living trees are attacked, the transpiration stream is interrupted, and the tree dies from the top downward   Blue stain is caused by several different fungi, but species of *Ceratostomella* or related genera are the most common ones   The genus *Ceratostomella* has been divided into two groups by von Hohnel (1918) who applied the generic name *Linostoma* to those species with obvious affinities to *Ceratostomella pilifera* (Fr) Wint   Because *Linostoma* had been used previously for a genus of flowering plants, Sydow (1919) substituted the name *Ophiostoma*   Goidanich (1934,

1936) divided the group still further by creating a new genus *Grosmannia*, based on the fungus described by Grosmann (1932) as *C penicillata*   For convenience the generic name *Ceratostomella* will be retained in this discussion

An association of insect injury with blue stain had been observed for many years, but the injury caused by insects was considered only as a weakening influence along with drought, fire, and other factors   Von Schrenk (1903) was perhaps the first to suggest that a blue-stain fungus is disseminated by beetles   He studied the association of the blue stain of western yellow pine
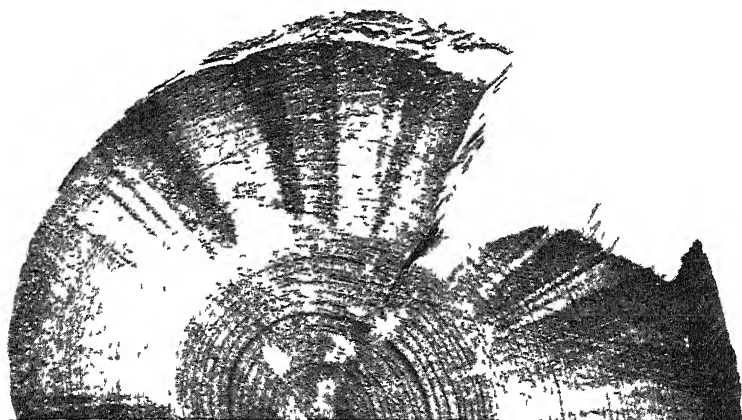
FIG 100 —A section cut from a log of red pine, the sapwood of which is affected with blue stain caused by *Ceratostomella ips* and transmitted by bark beetles

(*Pinus ponderosa* Lawson) with attacks of *Dendroctonus ponderosae* Hopk   He suspected that these beetles were disseminating the blue-stain fungus but was unsuccessful in isolating it from the insects and concluded that the spores were wind-borne and entered through the holes made by the beetles   No further study of the association was made until 1928 when Craighead called attention to the constant association of bark beetles (*Dendroctonus*) and blue stain in southern pine, pointing out that the direct injury caused by the beetles attacking living trees was not sufficient to cause the ensuing rapid death of the trees   He suggested that the blue-stain fungus was largely responsible for the death of the tree and that the fungus was probably introduced by the beetles   This hypothesis was proved

correct by Nelson and Beal (1929) and Nelson (1934) who showed that the fungus, artificially inoculated into the trees in the absence of the insects, would kill them in a relatively short time Rumbold (1930) described and named the fungus associated with
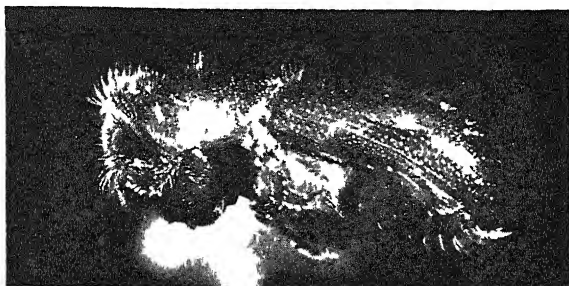
FIG 101 —A bark beetle (*Ips grandicollis*) caught and photographed as it emerged from a log infected with blue stain   Note the glistening white masses of spores of *Ceratostomella ips* adhering to its bristles   Histological studies have shown that the beetles are also internally contaminated and that viable spores are passed out in their excrement

these beetles *C ips*   Goidanich later referred it to his newly established genus *Grosmannia* [*Grosmannia ips* (Rumb) G Goid]   Grossman (1930) described and named several other
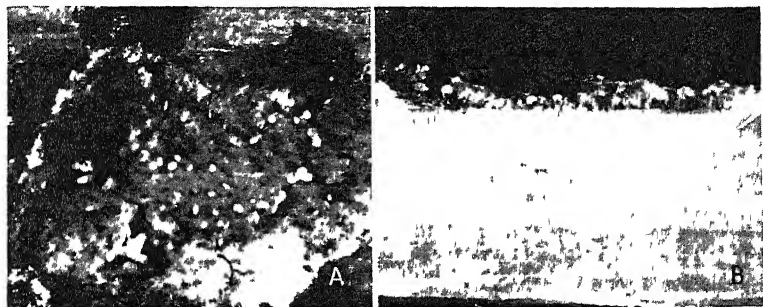
FIG 102 —Graphium coremia of the blue-stain fungus in the pupal chamber of *Ips pini*   A, as seen from above, B, as seen in section   Note the white sticky masses of spores borne on the tips of dark compound sporophores   The spores adhere readily to the beetles as they feed on the decayed inner bark   Approx 10 ×

blue-staining fungi and has studied in some detail their association with bark beetles in Europe

Experimental proof of the symbiotic nature of the association of *C ips* Rumb and two species of bark beetles (*Ips pini* Say and

I grandicollis Eichh) was presented by Leach, Orr, and Christensen (1934) who studied the details of the association throughout the life history of the beetles   Freshly cut logs of Norway pine (*P resinosa* Art) were exposed under a variety of conditions in experiments designed for determining the degree of interpendence between the beetles and the blue-stain fungi   The ends of some
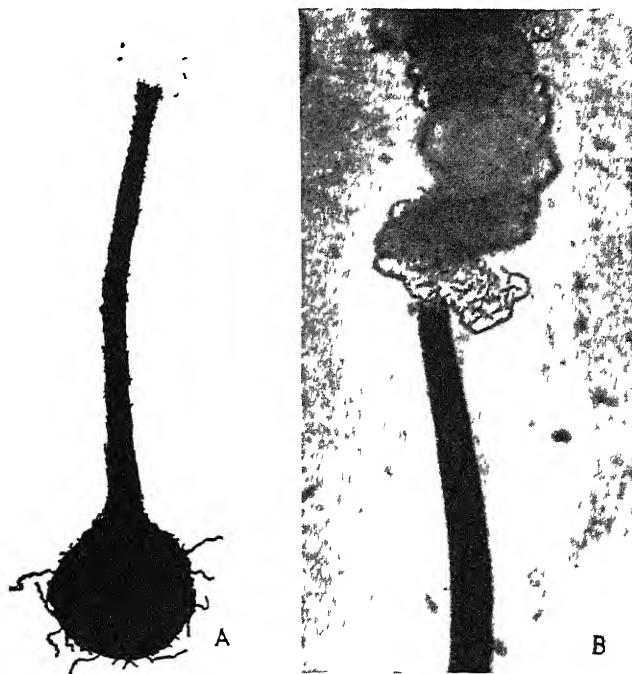
Fig 103 —*A*, a perithecium of *Ceratostomella ips* (approx 50 ×) , *B*, the tip of a perithecium mounted in water showing the ascospores oozing from the beak in a sticky matrix   Approx 75 ×

of the logs were sealed, and others were left without sealing   The logs were exposed in such a way as to exclude insects from some and to exclude wind-blown spores from others   It was proved by these experiments that the blue-staining fungi, along with certain yeasts, are universally introduced by the beetles and rarely, if ever, in any other way

The beetles, as they emerge from infested logs, are contaminated with the spores of the fungi both internally and externally (Fig 101)   Spores ingested by the beetles pass through the

intestinal tract and pass out in the excreta uninjured   As the
new brood of beetles develops, the fungus grows in the sapwood
and inner bark and fructifies on the walls of the tunnels and
pupal chambers   Both the conidia and ascospores of the blue-
staining fungi are borne in a sticky matrix in a way that ensures
thorough contamination of the new brood of beetles   The
conidia are borne in *Graphium* coremia in white sticky masses at
the apex of intertwined, dark-colored sporophores   The coremia
are often found on the walls of the pupal chambers or egg channels
(Fig 102)   The ascospores are borne in black, long-beaked
perithecia   In the presence of moisture, the ascospores ooze out

Fig 104 —Perithecia of *Ceratostomella ips*, growing on the wall of a bark beetle
tunnel, with their beaks pointing toward the center of the tunnel   Note the
white masses of ascospores on the tips

in white sticky masses (Fig 103)   The perithecia develop on the
walls of the tunnels with the beaks pointing inward, a position
well adapted for ensuring contamination of the beetles (Fig 104)
The new brood feeds in the fungus-infested inner bark for some
time before emergence, a habit that is conducive to both internal
and external contamination (Fig 105)

Thei e are usually two broods of the beetles, the first one emerg-
ing in midsummer   The freshly emerged beetles seek new trees
or logs, bore into the bark, and start new broods without any
intermediate feeding period   The second brood emerges in late
fall and spends the winter under the duff on the forest floor.
When the temperature rises in the spring, the overwintering
beetles emerge, bore immediately into suitable trees, and establish
new brood tunnels

The eggs of the beetles, which are deposited in niches along the sides of the brood galleries, are internally sterile, and no special anatomical structures in the insects to ensure congenital transmission of the fungus to successive generations have been observed The fungi apparently play no important part in the nutrition of the insect, but their presence in all probability makes the living tree a more suitable medium for beetle development by weakening the tree and reducing its water content   The fungi, by their action on the inner bark, also greatly modify the microenvironment of the developing brood of insects   The fungus obviously
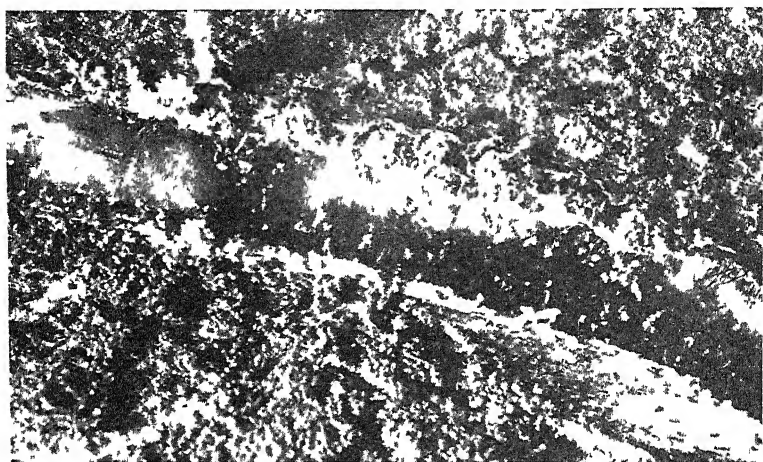
Fig 105 —A bark beetle (*Ips grandicollis*) feeding in an old tunnel prior to emergence   Note the bristlelike perithecia of *Ceratostomella ips* along the walls of the tunnel with their tips brushing the sides of the beetle   The beetles have been observed to feed upon the perithecia   Approx 4 ×

is dependent upon the insect for dissemination and penetration into the bark of the trees   In view of these facts, the association between beetle and fungus is considered one of true mutualistic symbiosis

In addition to *C ips*, a previously undescribed blue-staining fungus was found associated with the bark beetles in Norway pine by Leach, Orr and Christensen (1934)   This was an imperfect fungus forming relatively large ovoid spores in white waxy stromatic masses in the pupal chambers and old egg galleries (Fig 106)   This fungus, described and named *Tuberculariella ips*, when present was usually the predominating fungus in the

brood tunnels, although *C ips* was often associated with it   The fungus causes a blue stain of the sapwood indistinguishable from that caused by *C ips*

Person (1931) has shown that the yeasts associated with the beetles cause a fermentation of the sap and produce certain aromatic substances which, he thinks, may attract beetles to infested trees   This would account for the observed fact that the trees are always attacked by large numbers of beetles Trees with a few scattered beetle infestations are extremely

Fig 106 —Pupae of *Ips pini* surrounded by masses of spores of *Tubercularıella ips* growing on the walls of the pupal chambers   The beetles on maturity have been observed to feed on the spores many of which pass uninjured through their alimentary canals   Approx 3 ×

rare   In such isolated attacks, the beetles are usually drowned out by an excessive flow of sap and resin into the tunnels   The yeast associated with these and several other bark beetles infesting pines has been studied by Bramble and Holst (1935) and was described in detail by Holst (1936) who named it *Zygosaccharomyces pini*

It is probable that certain species of fungi are associated in some way with all bark beetles although the extent and the economic importance of the association may vary   Rumbold (1936) has recently shown that *C ips* is associated also with *Ips emarginatus* (Le C), *I integer* (Eichh), and *I oregoni* (Eichh)

on several species of conifers in the Pacific Coast forests   She
also has described two new species, *C piceaperda* associated with
D. piceaperda on spruce in eastern Canada, and *C pseudotsugae*
associated with *D pseudotsugae* on Douglas fir and larch on the
Pacific Coast   The extremely destructive Dutch elm disease
is caused by an association of the several species of elm bark
borers and *C ulmi* (Schw) Buisman   In many respects, the
relationship is strikingly similar to that between the bark
beetles of conifers and the blue-staining fungi

Wright (1935) has described still another association between
a bark beetle and a wood-staining fungus   *Scolytus ventralis*
Le C , a bark beetle infesting white fir (*Abies concolor* Lindl and
Gord) in California is often fatal to the trees   A brown stain
associated with the tunnels was found to be caused by a species
of *Trichosporium*, later proved to be pathogenic to fir trees
The fungus (named *T symbioticum*) was found to be regularly
transmitted by the beetles in a manner similar in all essential
respects to that described above for the blue-staining fungi
Wright concludes that the association between fungus and
insect is mutually beneficial and interprets the relationship
as one of mutualistic symbiosis

In a later report, Wright (1938) described a similar association
between a brown-staining fungus [*Spicaria anomala* (Corda)
Harz] and two additional species of beetles (*Scolytus praeceps*
Le C and *S subscaber* Le C) affecting white fir   These two
beetles commonly infest the tops and branches of the trees,
respectively, whereas *S ventrales* is found mostly in the base of the
tree   *Trichosporium symbioticum* was found only in the base
of the tree, and *S anomala* was limited to the tops and branches
It was shown that the fungi would grow in any part of the tree
when artificially inoculated   Therefore it was concluded that
the occurrence of the two fungi in different parts of the tree
was due entirely to their association with their respective vectors
Both fungi killed the cambium in advance of the beetles and
caused a marked reduction in moisture content of the sapwood,
a condition considered favorable for the successful establishment
and maintenance of individual beetle broods

The Dutch Elm Disease —In 1919, a destructive disease of
elm trees was discovered in Holland and described by Spierenberg
(1922)   In the next few years, the same disease was reported

fiom piactically all the counties of Central and Southern Euiope It was discovered in England in 1927 (Wilson and Wilson 1928) and in the United States in 1930 (May, 1930, 1931)

Fig 107 —An elm tree affected with the Dutch elm disease (*Reproduced from U S Department of Agriculture Circ 322, Outbreaks of Dutch Elm Disease in the United States, by Curtis May*)

As the disease was first recognized in Holland, it has been known generally as the "Dutch elm disease" It is extremely destructive, and practically all species of elms are susceptible Because of the value of the elm as a shade tree, the disease has been the subject of extensive investigation in every country where it has been found

Affected trees may be killed rapidly, dying within 1 or 2 years after infection   In other cases, the disease acts slowly and may not kill the tree for several years   The first symptoms are a wilting and drying of the leaves of terminal branches   The leaves usually drop prematurely from affected branches, only the very young terminal leaves persisting after the normal time for abscission (Fig   107)   The most characteristic diagnostic symptom, although not an infallible one, is a brown discoloration in the outer annual growth rings of the sapwood of affected branches
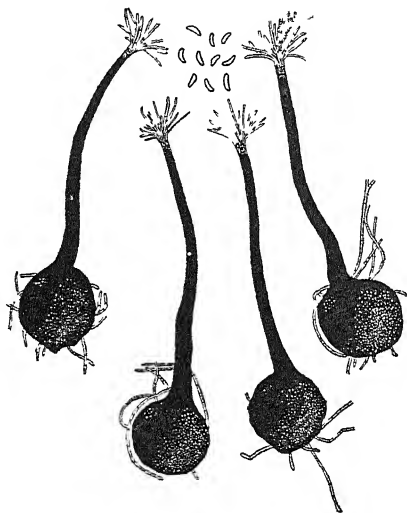
Fig   108 —Perithicia of *Ceratostomella ulmi*   Approx   122 ×   (*After Buisman*)

The discoloration may appear as a continuous or partial ring, as an arc, or as a ring made up of separate brown dots

The Dutch elm disease is caused by a fungus, first described in the imperfect stage by Schwarz in 1922 as *Graphium ulmi*   The perfect stage was discovered and described by Buisman (1932) as *Ceratostomella ulmi* (Schw) Buisman   It was later referred to the genus *Ophiostoma* (Nannfeldt 1932)   The fungus is closely related, and very similar, to the fungi causing blue stain of coniferous trees which are disseminated by the pine bark beetles (Fig   108)

The method of dissemination of *C   ulmi* was not known for several years after its discovery   Marchal (1927) and Wollenweber and Stapp (1928) were the first to point out the possible

significance of insects in the spread and development of the disease These authors found the pathogen fruiting abundantly in the pupal chambers and galleries of the bark beetle (*Scolytus scolytus* Fabr) This discovery, together with the constant association of the disease with the insect attacks and certain observations on the sporadic appearance of the disease near older infected trees, led them to the assumption that the insect was a vector of the disease The correctness of this assumption has since been verified by numerous workers, including Betrem (1929), Fransen (1931, 1932, 1935, 1939), Fransen and Buisman (1935) In addition to *S scolytus* Fabr *S multistriatus* Marsh was soon shown to be an important vector (Fransen 1932, Collins 1935, Collins *et al* 1936) The latter insect is the principal vector of the disease in the United States where *S scolytus* has not yet become established Another species of *Scolytus*, *S sulcatus* Le C , has been found in and near the region of Dutch-elm-disease infestation and is considered as a possible vector of much importance The biology of the beetle has been studied by Pechuman (1938) who points out that its life habits are very similar in many respects to that of *S multistriatus* The apple is its preferred host, but it breeds also in elm, in mountain ash, and in peach trees Like *S multistriatus*, it has the habit of feeding on the crotches of young twigs of vigorous trees before seeking weakened trees in which to breed and in this respect should be an effective vector of the disease

Several other genera of insects have been incriminated in the spread of the disease or have been proved to be potentially important, but the bark beetles appear to be the principal vectors in all countries where the disease is known In addition to the above-mentioned species of bark beetles, *S sulcifrons* Rey , *S affinis* Egg , *S laevis* Chap , and *S pygmaeus* F are said to be important vectors in Europe (Goidanich and Goidanich 1934, Kalandra and Pfeffer 1935) Collins *et al* (1935) have shown that the native American elm bark beetle (*Hylurgopinus rufipes* Eichh) is also a vector, but it probably is not so effective as the species of *Scolytus* In addition to the bark beetles, the following insects also have been mentioned as vectors, with less convincing proof *Ptelobius vittatus* F , *P kroatzi* Eichh , *Saperda punctata* L , *S tridentata* Oliv , and *Magdalis armigera* Geoff

The significance of *Saperda tridentata* as a vector has been investigated by Tyler, Parker, and Pechuman (1939)   This insect is prevalent in the area of Dutch-elm-disease infestation near New York, N Y   It breeds in the bark of diseased elms, and many adults caught after emerging from the bark were found to be contaminated with *C ulmi*   Inasmuch as the adults feed
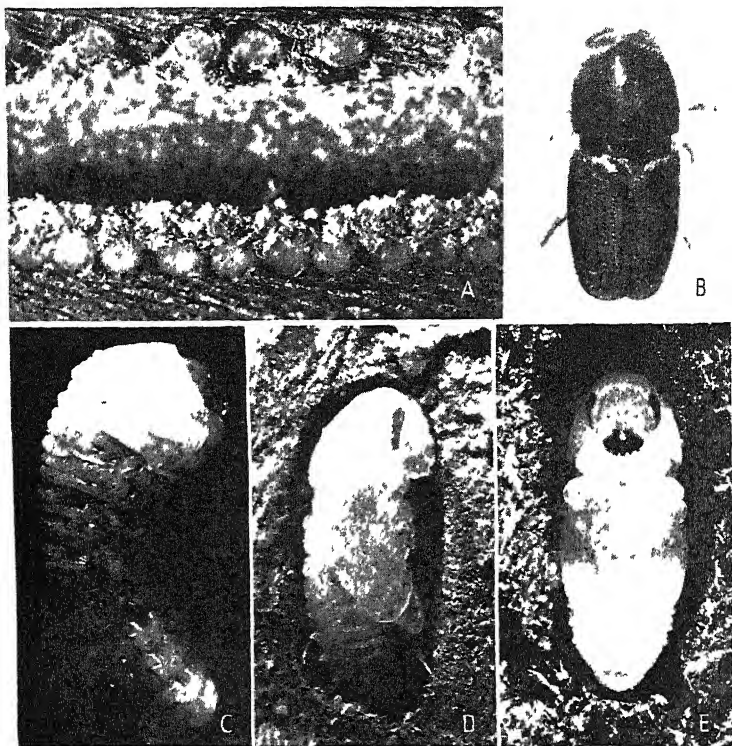
FIG 109 —Life stages of the elm bark beetle (*Scolytus multistriatus*)   *A*, eggs as they are deposited in niches along the brood tunnel, *B*, an adult beetle, *C* a larva, *D*, a pupa, lateral view, *E*, a pupa, ventral aspect   13 ×   (*After Readio*)

on leaf blades, mid-ribs, petioles, and succulent elm shoots, it has abundant opportunity to transmit the disease   It was shown experimentally that the feeding wounds made by feeding adults could serve as avenues of entrance for the pathogen   Also, infection was obtained by subjecting young elms to beetles that had been artificially contaminated with spores of the fungus

No successful inoculations with naturally contaminated beetles were reported   It is to be concluded from this work that the insect is a potential vector, but its significance in nature remains to be determined

A comprehensive account of the disease and a review of the pertinent literature is given by Clinton and McCormick (1936) The most complete study of insect transmission and the biology of the elm bark beetles in Holland is that of Fransen, an extensive account of which was published in 1939   Good descriptions of the disease and its insect vectors in the United States have
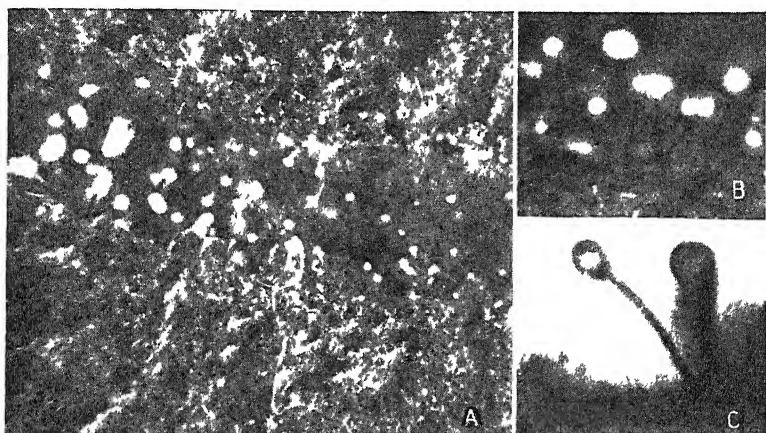
Fig 110 —Coremia of *Ceratostomella ulmi* in the egg galleries of an elm bark beetle   The white sticky masses of spores adhere readily to the insect's body, but are not adapted to dissemination by other means   (*After Clinton and McCormick*)

been published also by Welch, Herrick, and Curtis (1934), Readio (1935), and by McKenzie and Becker (1937)   Collins (1938) has mapped the known distribution of *S multistriatus*, *Hylurgopinus rufipes*, and the disease in the United States as of 1937   The former species was known to occur in three distinct centers of infestation one in eastern Massachusetts and southern New Hampshire, one in New York, New Jersey, Connecticut, southwestern Massachusetts, Delaware, and eastern Pennsylvania, and one along the Ohio River in western Pennsylvania, southern Ohio, West Virginia, southern Indiana, and northern Kentucky   The beetle was found in five locations in eastern West Virginia and in one location just across the Potomac

in Maryland   *Hylurgopinus rufipes* is generally distributed
throughout the eastern part of the United States and Canada
It probably extends throughout the range of the elm   In
1939, the disease was known to occur in a major area of infection
near New York, N Y , and in New Jersey and Connecticut and
in several scattered infections in Maryland, Ohio, Indiana, and
West Virginia

The smaller European elm bark beetle (*S   multistriatus*)
(Fig 109) breeds in and under the bark of elm trees   In general,
it breeds only in trees that are weakened by disease, drought,
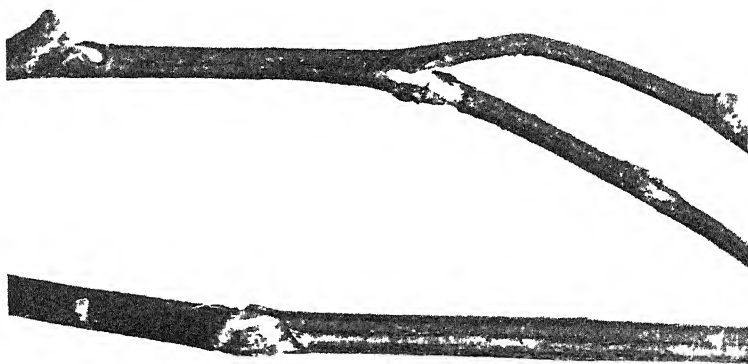
Fig 111 —Crotch feeding wounds made by *Scolytus multistriatus* after
emerging from a diseased tree and before entering a new tree to establish a brood
gallery   Much of the initial infection of elm trees takes place here   (*After
McKenzie and Becker*)

or other unfavorable conditions   The insect survives the winter
in the larval stage under the bark, and the new brood of beetles
emerges in early spring   Before entering the bark of other trees
to establish brood tunnels, the beetles feed for about ten days
on the inner bark of the tender twigs of healthy vigorous elm
trees   Numerous investigators have shown that the elm-disease
pathogen fruits in the old brood and larval tunnels and that the
beetles emerging from diseased trees are practically always
contaminated with the spores both internally and externally
Spores borne in sticky masses on *Graphium* coremia constitute
the chief source of contamination (Fig 110)   The contaminated
beetles may inoculate the tree in the feeding wounds on young

branches (Fig 111), or the fungus may be introduced by the beetles when they bore into the bark to establish brood tunnels The brood tunnels (which are characteristic for each species of *Scolytus*) always run parallel to the grain of the wood and are 1 to 2 inches in length (Fig 112)   The eggs are laid in small niches along the sides of the tunnel (Fig 109*a*)   The larvae, on hatching, bore out at right angles, but, as they enlarge, their tunnels spread out so that those arising at the ends of the main tunnel may be parallel to the grain when the larvae mature (Fig 112)   The pupal chambers are formed at the end of the
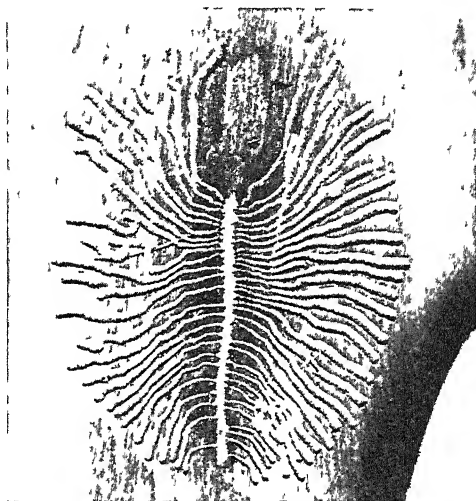
Fig 112 —A complete brood gallery of *Scolytus multistriatus* in the bark of a diseased elm tree   (*After McKenzie and Becker*)

larval tunnels, and when the adults mature they bore circular holes in the bark through which they escape   There are usually one or two broods of the beetles, the second brood serving to carry the insect over winter as larvae or pupae under the bark (Fig 109)   The larger European elm bark beetle (*S scolytus*) according to Fransen (1939) has two to four broods per year

The relationship between elm bark beetles and the Dutch elm disease is similar in many respects to that between the bark beetles of coniferous trees and the blue stain of conifers   The chief point of difference is in the feeding habits of the adult beetles   The pine bark beetles (*Ips spp*) feed for a time on

the old inner bark before emerging and do not feed on the twigs before entering a new tree to establish brood tunnels This difference in feeding habits is of great significance in the economic importance of the two diseases Both groups of insects require weakened trees for the establishment of blood tunnels and usually attack such trees in a gregarious manner The pine bark beetles depend upon drought, fire injury, or other adverse factors for providing the weakened trees The elm bark beetles, on the other hand, by their habit of feeding on the tender twigs of vigorous, healthy trees before breeding in the weaker trees, inoculate the vigorous trees with the pathogen By the time a new brood of insects emerges from the infested trees, the vigorous trees that were inoculated by the feeding beetles have been weakened by the fungus and provide additional breeding places for the insect Thus a vicious circle is established that makes the elm disease destructive to vigorous trees, while the blue-stain disease of pines remains largely a disease of trees that have been weakened previously by some other factor

The native elm bark beetle (*H rufipes*) rarely ever feeds upon the twigs of healthy trees before entering the bark of weakened ones to establish breeding tunnels, and for this reason it has been considered of relatively little importance as a vector However, Kaston and Riggs (1938) have shown that this species usually makes a short feeding tunnel through the bark of the trunk and larger branches of healthy trees and feeds for a while on the inner bark (Fig 113) before establishing brood tunnels The significance of these feeding tunnels in the transmission of the disease has not yet been determined, but they are of much potential significance Kaston (1939), who has published a complete account of the life history and habits of this insect, considers them "analogous to the well-known crotch and twig feeding injuries of *Scolytus multistriatus*, and hence important in relation to the spread of the Dutch elm disease "

D L Collins (1938) has studied the feeding habits of *S multistriatus* from the viewpoint of its role as a vector He has shown that the distribution of feeding wounds on trees in generally infested areas is very erratic In general, the trees near infested trees and those near weakened trees that are attractive as breeding places are more subject to feeding wounds, and consequently to infection, than those not so situated

The numerous associations between bark beetles and fungi that have been described suggest that the association is a general one, but the sudden appearance of the Dutch elm disease in western Europe where the elm bark beetles have been known for a long time seems to indicate that this particular association is not one of long standing   This view is further supported by the fact that *S multistriatus*, an active vector of the disease, was introduced into the United States in the vicinity of Boston, Mass , prior to 1909 (Chapman 1910) and became established
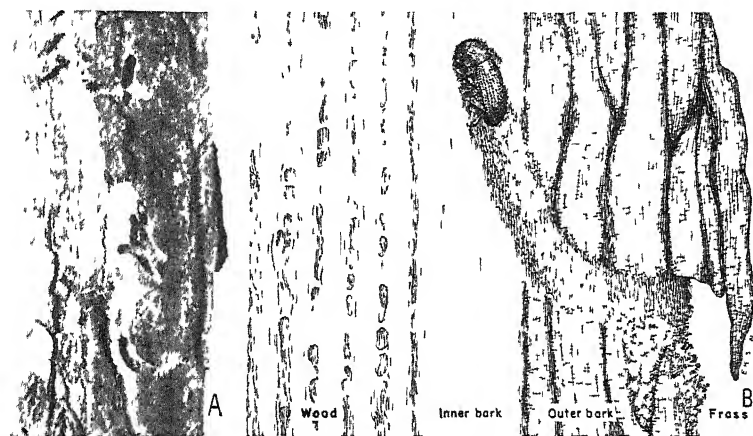
FIG 113 —Shallow feeding tunnels made by *Hylurgopinus rufipes* in the bark of an elm tree   These tunnels are never extensive and are distinct from the breeding galleries made in weakened trees   *A*, a surface-view photograph, *B*, a diagrammatic section of a feeding tunnel   Note that the tunnel extends into the inner bark but not into the sapwood   (*After Kaston and Riggs*)

there, but the disease was not introduced with it   However, when the same insect was introduced near New York, N Y , after the disease had appeared in Europe, the disease also was brought in   These facts suggested the theory (Leach 1935) that the Dutch elm disease as a serious economic factor may have had its origin in Western Europe as a result of the association of the beetles with a new fungus which was not a serious pathogen in the absence of a suitable vector   The association of some sort of fungus with bark beetles appears to be so general that it is only reasonable to suspect that *C ulmi*, because of its greater efficiency in providing breeding places for the beetles, is replacing a less efficient fungus symbiote   In view of this very general associa-

tion of bark beetles with fungi, it would be interesting to know what fungi, if any, are associated with the beetles in regions where the Dutch elm disease does not occur

The discovery of Walter (1937) that there are nonpathogenic strains of *C (Graphium) ulmi* suggests the possibility that the pathogenic strains may have arisen by mutation from a previously harmless fungus symbiote of the beetle   If this were true, the nonpathogenic strains might be found associated with the beetles in the disease-free areas   In so far as the author knows, no study of the fungi associated with the beetles in disease-free areas has been published

The possible role of mites as vectors of the Dutch elm disease has been discussed by Jacot (1934, 1936)   Tyroglyphid mites which are themselves transported in the hypopial stage from tree to tree by insects that breed in the bark of infected trees, are potential vectors, but their importance in this respect was not determined by Jacot   Fransen (1939), also, has described the association of mites (*Pseudotarsonemoides innumerabilis* Vitzth) with the elm bark beetles and *C ulmi*   According to Fransen, the mites transport the spores of the fungus from the egg galleries to the walls of the pupal chambers and, by their activity, stimulate the fungus to sporulate more profusely than it does in the absence of the mites   For a more complete discussion of mites as vectors of this and other diseases, see Chap XI

The association of a destructive plant disease such as this one with insect vectors adds much to the complexity of the problem of control   Attempts are being made to eradicate the Dutch elm disease in the United States   In Holland and other European countries, earnest efforts are being made to protect the remaining elms by controlling the beetles and protecting the elms against beetle attack   The success of these efforts depends upon many factors, one of the most important of which is a thorough knowledge of the pathogen, its vectors, and the intricate association of the two   Because of the economic and aesthetic value of the elm, extensive and thorough investigation of the disease is imperative

Fig Diseases —In California, the fig is affected by a group of diseases commonly referred to collectively as "fruit spoilage diseases '   These diseases are largely dependent upon insects for their spread and development   They are destructive and

often cause enormous losses   The three most common diseases are *endosepsis, smut,* and *souring*

Endosepsis, an internal rot of the fig fruit, was first recognized and described by Caldis (1925 1927), who studied it in California from 1922 to 1925   The disease was prevalent and destructive in 1927 and has been troublesome since then   Endosepsis affects only the caprified fig, and the fig wasp (*Blastophaga psenes* L) (Fig 114) is the principal vector of the fungus pathogen (*Fusarium moniliforme* var *fici*)
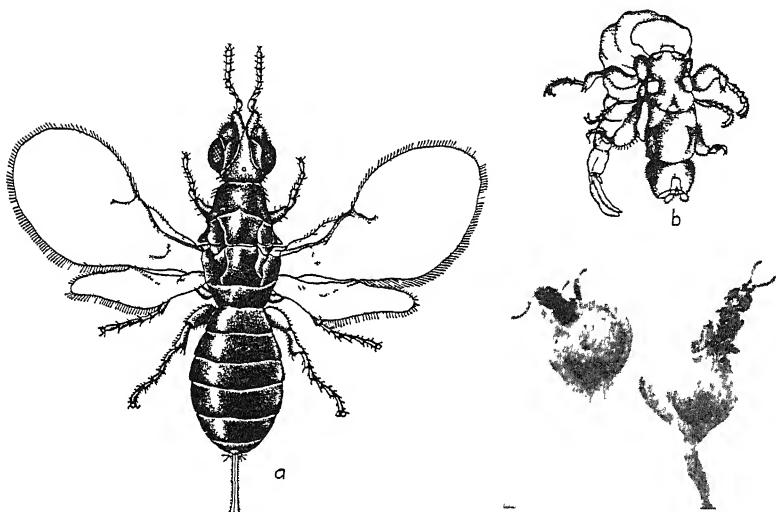
Fig 114 —The fig wasp (*Blastophaga psenes*)   *a,* female *b,* male *c,* a male and female emerging from galls from a caprifig   The female is impregnated by the male before she emerges from the gall   On leaving the fruit the female becomes dusted with pollen from the staminate flowers that surround the opening   If the fruit is diseased the insect may also become contaminated with spores and transport them to healthy fruits of the edible fig   (*After Smith and Hansen*)

In order to understand the relation of the insect to the disease, it is necessary to know the life history of the insect and its relationship to the development of the fig fruit   This relationship is briefly and clearly presented by Smith and Hansen (1931)   The fig "fruit" is in reality an aggregation of fruits borne in the cavity of a hollow receptacle, known botanically as a "synconium" (Fig 115)   The caprified fig of California is of the Smyrna type, and is a dioecious, insect-pollinated plant   The synconium that becomes the edible fruit bears no pistillate flowers, whereas the caprifig has both male and female   The caprifig has three crops

of fruit each year   The first or spring crop is called the "pro-
fichi," the second or summer crop the "mammoni," and the third
or fall crop the "mamme"

The *Blastophaga* insects live over winter in the galls or enlarged
florets of the mamme crop   In early spring, the male *Blastophaga*
emerge from the galls and fertilize the females while the latter
are still in the galls (Fig 114)   After the females have been
fertilized, they emerge, leave the old mamme fruits, and enter the
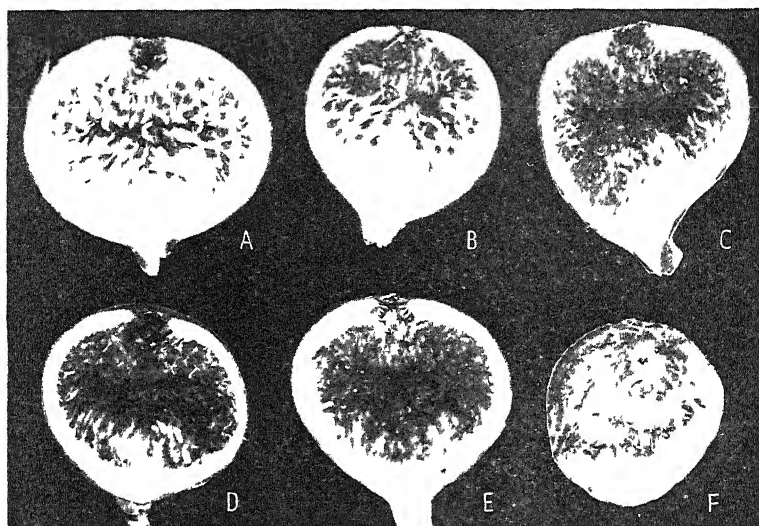
Fig 115 —Endosepsis of Calimyrna figs   *A*, a sound fig fruit consisting of a
hollow fleshy receptacle with an aggregation of flowers or fruit arising from its
inner wall, *B*, an early stage of endosepsis with only the flowers around the "eye"
affected, *C − E*, more advanced stages of endosepsis, *F*, external view of a badly
diseased fruit   (*After Smith and Hansen*)

young developing profichi crop   Here they oviposit in the ovules
of the young flowers   The eggs hatch, and the larvae develop
and pupate in the galls formed from these flowers   This new
brood of insects is ready to emerge in early summer when the
crop of figs on the edible-fig trees is developing   When the
female insects leave the profichi figs, they rub against the stami-
nate flowers which surround the opening in the fruit and become
covered with pollen (see Fig 24)   The insects carry the pollen
into the undeveloped edible fruit and pollinate the flowers while
seeking a place to oviposit   Oviposition, however, is not effected,

because the styles of the flowers in the edible fig are too long
The flowers, however, are successfully pollinated, and the fruits
develop normally   Some of the insects enter the third, or
mamme, crop of figs where they pass the winter as larvae or pupae
in the galls   Various kinds of special manipulation are practiced
by growers to ensure caprification of the crop of edible figs
Usually the profichi crop is collected when the females are ready
to emerge, and the figs are hung in wire baskets in the branches
of the edible-fig trees

Endosepsis is a firm dry rot of the fig fruit (Fig 115)   It is
not easily detected from the exterior until the fruit begins to
ripen   The affected tissues are water-soaked at first, becoming
brown with a tinge of pink color   In later stages, the fruit is
dry, seedy, and tasteless   There is no fermentation or souring
of the tissues associated with endosepsis

Caldis has shown that the spores of the pathogen are introduced
into the edible fig by the *Blastophaga* insect   The fungus infects
and sporulates also in the tissues of mamme and profichi fruits
The insects are usually contaminated with the spores as they
emerge from the infected fruits   The fungus is not associated
with the eggs, larvae, or pupae   The adults are contaminated
only after they emerge from the galls   Caldis proved experi-
mentally that figs pollinated by insects from noninfected caprifigs
remain healthy, but when pollinated by insects that come from
infected caprifigs the fruit becomes diseased with endosepsis
Two species of bacteria are constantly associated with the fungus
and are also disseminated by the insect, but neither species
appears to be pathogenic   The fungus (*Fusarium moniliforme*
var *fici*), however, is pathogenic when used in pure culture as
inoculum

Hansen (1927, 1928) demonstrated that caprifigs could be
successfully disinfected without injury to the insects by washing
the interior of the fruit with a 0 2 per cent solution of Semesan
while the insects were still in the galls in the larval or pupal stages
This treatment appeared to be practical when applied to the
mamme crop so that the profichi crop would be infested with
noncontaminated insects

Some success in the control of endosepsis has been obtained in
the use of the treatment by the growers   In 1928, an effort was
made to use the method on a large scale under state supervision

More than 60 tons of the mamme crop was collected and sent to
a central station where it was treated and incubated until the
Blastophaga emerged to be caught in glass tubes and returned to
the orchard for caprification of the profichi crop   The effort
appears to have been somewhat premature for such large-scale
operation, and although there was some evidence of control of
the disease, the project was not entirely successful   The disease-
control program resulted in a scarcity of insects for pollination,
and there was a very poor set of fruit   The loss from the short
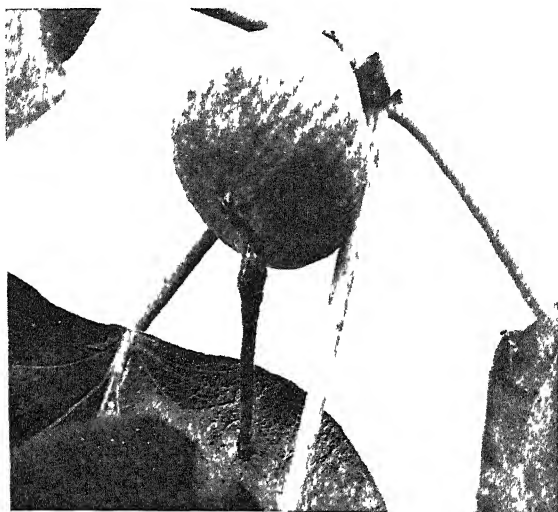
Fig 116 — A fig fruit affected with ' souring "   Note the exudate from the eye
(*After Smith and Hansen*)

crop offset the gain through disease control   With more experi-
ence and better technique, the control through disinfection of the
mamme crop may prove practical

Souring is a term applied to the fermentation of the sugary sap
of figs by two or more species of yeast and the resulting decom-
position and contamination by bacteria and molds   Souring
affects both the common parthenocarpic fig and the caprifig, but
it is most typically a disease of the former which, because of its
independence of the fig wasp, is not affected by endosepsis   The
disease is often very destructive, sometimes causing a loss of
more than 50 per cent of the crop

Souring is a disease of the ripe fruit   The normally pink flesh loses its color and becomes water-soaked and translucent   Odors characteristic of alcoholic fermentation followed by that of acetic acid are characteristic   Gas bubbles form in the pulp, and a jellylike exudate flows from the "eye" (Fig 116)   A white scum of yeast is often evident on the surface of the affected tissue When the fruits dry before destruction is complete, the base of the fruit dries to a black shriveled mass to which the term "black neck" is often applied   Small cankers are formed on the stem at the point of attachment if the fruit does not drop

The work of Smith and Hansen (1927), Caldis (1930), and Hansen (1929) has shown that the yeasts responsible for souring, as well as the secondary fungi that follow, are introduced largely, if not entirely, by insects   The most important of the vectors of souring are the dried-fruit beetle (*Carpophilus hemipterus* L) (Fig 117) and the fruit fly (*Drosophila ampelophila* Leow) Both these insects feed on, and breed in, decaying citrus fruits, melons, etc , where they have ample opportunity to become contaminated with yeast   When the "eye" of the fig is open, these insects enter in search of food and carry the yeast and fungus spores with them   The disease has been produced by caging the dried-fruit beetle with healthy fruits, and fruits have been protected from the disease by excluding the insects   Caldis (1930) has shown that the yeasts are transported both externally and internally by the dried-fruit beetle

Hansen and Davey (1932) have demonstrated that several species of thrips and mites enter young fruits even before the eyes are "open" and that they introduce spores of several different species of mold as well as a few yeasts in about 15 per cent of the cases   Unsuccessful attempts to introduce spores into the interior of the figs by forcibly blowing them against the eye with an atomizer strengthen the conclusion that insects are the chief agents of inoculation and that wind is of little importance Because the dried-fruit beetle as well as the fruit flies breed in decaying fruits, the destruction of any waste fruits that might serve as breeding places is recommended as the most important control measure

Smut of figs is not a true smut but a mold, being caused by a strain of *Aspergillus niger*   It is one of the oldest and best known

diseases of the fig   It has been known in Southern Europe for
many years and is mentioned in the earliest records of the fig
industry   All kinds of fig are affected, but smut is most common
on caprified figs

In the earlier stages of smut, small, brown, soft spots are
formed on the interior flesh   In later stages, when the fruit is
ripe or even after drying, masses of black spores are formed
Through the work of Hodgson (1918) and Phillips, Smith, and
Smith (1925), it has been proved that the spores of *Aspergillus*

Fig 117 —Dried-fruit beetle (*Carpophilus hemipterous*) emerging from a decay-
ing orange fruit   Such insects are thoroughly contaminated with yeasts, molds,
and other microbes   When they enter the fig fruit, diseases such as souring or
smut usually follow   (*After Smith and Hansen*)

are introduced into the figs chiefly by the dried-fruit beetle (*C
hemipterus* L) (Fig 117) and to a lesser extent by *D ampelophila*
Leow   According to Hansen and Davey (1932), thrips and mites
enter the very young fruits, and it has been shown that they may
introduce spores of *Aspergillus* as well as other fungi

The control of smut, like the control of souring, depends upon
reducing the number of contaminated beetles and thrips that
reach the fig fruits   The destruction of waste fruits that serve
as breeding places for the beetles and the fungi is recommended

Perennial Canker of Apple and the Woolly Aphis —In 1925,
Zeller and Childs described a disease of apples in Oregon caused
by a fungus, which they named *Gloeosporium perennans*   The

disease causes both a rot of the fruit and a canker of the branches
The cankers are characterized by successively formed concentric
rings of callus growth (Fig 118)   The fungus grows actively in
the cankers during the late winter months, when the callus formed
the previous season is invaded and killed   In the summer, the
pathogen is inactive, and the canker heals, forming a new ring
of callus which in turn is killed by the fungus the following winter
This progressive, year-to-year expansion of the canker led Zeller
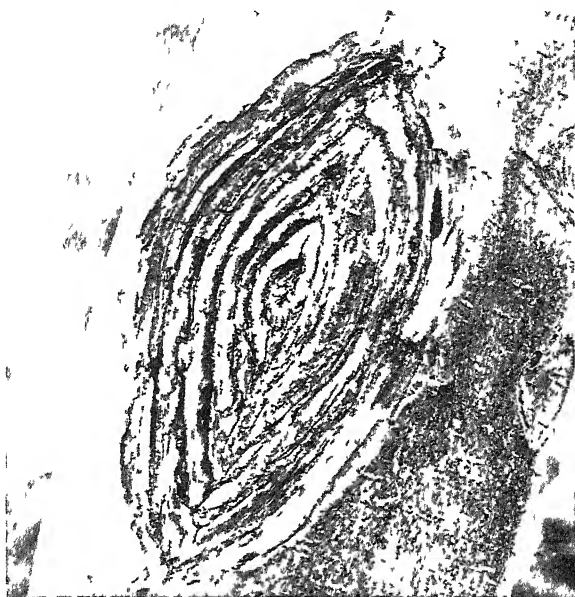
Fig 118 —A large perennial canker of apple showing the numerous annually
formed callus rings   After each year's growth of callus the pathogen is com-
pletely walled off and reinfection is dependent upon the feeding wounds of the
wooly aphis   (*After McLarty*)

and Childs to name the disease "perennial canker "   Childs
(1929) and McLarty (1933) demonstrated that in spite of the
perennial character of the canker the infection is really annual in
nature   They showed that in summer, when a new callus was
being formed, the pathogen was completely shut out of the living
tissues so that a new infection was necessary for the further expan-
sion of the canker   Since the fungus may live for several years as
a saprophyte in the dead bark and may sporulate abundantly, it
is universally present in old cankers but is unable to reinfect

without the aid of some wounding agency   McLarty (1933) has
shown that the necessary wounds are provided by the wooly
aphis (*Schizoneura lanigera* Hausmann) which commonly feeds
on the newly formed callus tissue (Fig 119)   Small blisterlike
galls of delicate tissue are formed where the aphids feed   Upon
freezing, these galls rupture and provide the wounds through
which the fungus reinfects

The original, or primary, infection of the branches occurs
chiefly through pruning wounds and usually follows aphid infesta-
tion of the callus formed on the wound   Small "button cankers"
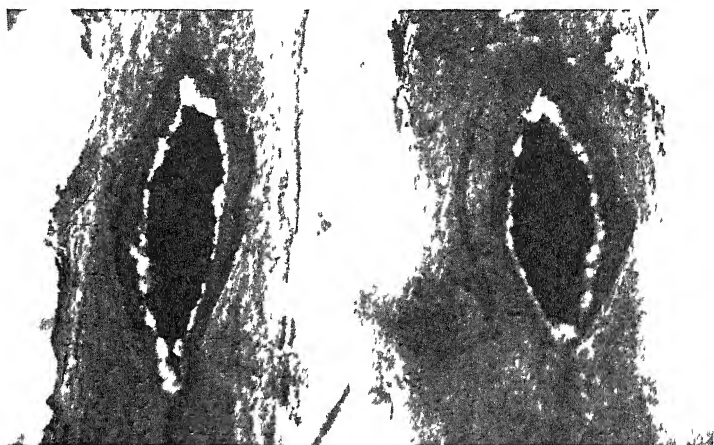
Fig 119 —Two young perennial cankers showing the wooly aphis feeding on the
tender callus tissue   (*After Childs*)

are often produced as a result of direct infection through the
lenticels, but these are very superficial and, because they are
not attractive to the aphids, usually persist for only 1 year and
then heal over completely   There is no experimental evidence
to show that the aphids disseminate the fungus, but it is believed
by many observers that they do so to some extent

The life history of the woolly aphis is somewhat complicated
and is not completely known   It can live on both the roots and
the aboveground parts of fruit trees as well as on the foliage of
the elm, where the winged forms and the egg-laying generation
occur   Eggs are deposited in crevices of the elm bark where
they survive the winter and hatch in the spring   The insects
map also survive the winter as adults in the cankers on apple

trees   Small swellings are caused on the roots of the apple trees, but these are soon destroyed by decay   The cause of this decay of infested roots has never been determined

The association of the woolly aphis with this disease is not entirely fortuitous, for there is a measure of mutualistic symbiosis involved   The crevices and old bark of the cankers provide protection for the aphids against predators, parasites, and other unfavorable factors of the environment (Fig 120)   In turn, the aphids provide the wounds necessary for reinfection, and
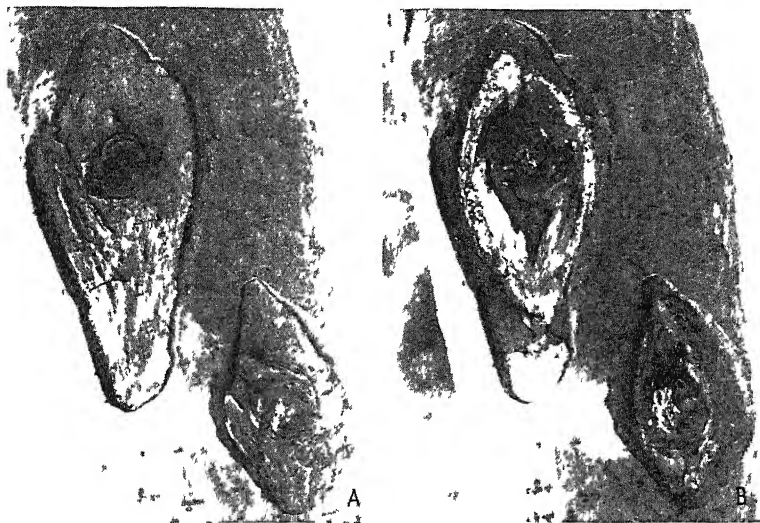
FIG 120 —*A*, perennial cankers after 1 year's growth, still covered with the dead bark, *B*, the same cankers with dead bark removed to show the wooly aphis to which the canker affords both food and shelter   (*After Childs*)

in the expansion of the canker and the resulting callus additional food and protection for the aphids are provided   Thus the insect and the fungus are mutually benefited by the association

A knowledge and appreciation of the part played by the aphids in the development of the cankers have helped in the control of the disease   Control of the canker has been accomplished largely through the control of the aphids   More rigid inspection of nursery stock for aphid infection is practiced, and aphids are controlled in the orchard by spraying and by cleaning out the old cankers, so that the protection for aphids will be reduced to a minimum   Cankers formed by stub pruning offer less protec-

tion for the aphids than those formed by close pruning, and stub pruning therefore is recommended In Oregon, when cankers are cut out later than February, no extension of the canker takes place, for the incipient infection is removed, and new, vigorous, uninjured callus growth follows It has been observed that the Northern Spy variety is resistant to the aphid and is also relatively free from perennial canker

European Canker and the Woolly Aphis —Although the details of the association have not been worked out so thoroughly as they have with respect to perennial canker, evidently a similar relationship exists between the European canker and the woolly aphis European canker caused by *Nectria galligena* is essentially the same type of canker, the pathogen becoming active in late winter and the canker healing in summer The close association of these insects with the European canker has been observed for a long time, but their importance in the development of the canker has not been extensively studied Wiltshire (1915), however, described the galls made by the aphids when feeding on the callus in the cankers and concluded that infection probably occurred through the wounds made by the collapse of the galls, rather than through the earlier feeding punctures He also noted that cankers usually occur in the year following that of heavy aphid infestation Cotton (1918) discussed the probable relationship of aphids to the canker as follows

Probably one of the most frequent methods by which the fungus gains admission is through injuries caused by the woolly aphis The soft, swollen tissue produced by the aphids is very apt to become cracked during the winter and it is probable that when the aphis returns the following season to the wounded area, *Nectria* spores are attached to their bodies and introduced into the cracks with the aphis

Cunningham (1923) has reported in New Zealand a canker of apple caused by *Diplodia griffoni* He concluded that infection is effected chiefly through wounds made by the woolly aphis and that the fungus is also disseminated to a great extent by the insect The relationship between insect and fungus is probably very similar to that described for perennial canker

Bees and the Downy Mildew of Lima Beans —Sturgis (1898) has shown that bees are the principal agents in the dissemination of downy mildew of lima beans, caused by *Phytophthora phaseoli*

Thaxter   The disease, which was first described by Thaxter in 1889, was reported as very destructive in wet seasons in Connecticut   Sturgis (1898), following a severe outbreak of the disease in 1897, reported that one of the most serious aspects of the disease was the infection of the young ovary before the fall of the blossoms   Careful observations led him to conclude that bees, which normally pollinated the flowers, were largely responsible for this floral inoculation   He noted that the young pods became infected only at the base of the ovary and on the

FIG 121 —Bean blossoms showing the method of inoculation with downy mildew (*Phytophthora phaseoli*) through the agency of bees   *A*, a normal flower with all parts in position before pollination, *B*, a flower with keel depressed and style protruded after it has been visited by a bee, *C*, a sectional view of the flower with petals removed to show ovary, *D*, ovary from an infected flower showing mildew growing and fruiting on the style and at the base of the ovary, the two points of contact with the insect   (*After Sturgis*)

style and that these were the two points where the bee in search of nectar touched the more moist and delicate tissues of the flower

A good visualization of this relationship can be had by an examination of the flower parts shown in Fig 121   When a bee alights upon the flower, its weight deflects both the wings (*B*) and keel (*C*) and causes the style to protrude from the keel and to touch the bee   In seeking the pollen, the bee's head brushes the base of the ovary   This is an adaptative mechanism that ensures pollination, but it also facilitates the inoculation of the young pod with the spores of *Phytophthora phaseoli*   The

style and the base of the ovary are fully protected by the petals until exposed by the bees in this way, but it is at exactly these points that the young pods are infected by the fungus

Plant Bugs and Stigmatomycosis —A characteristic type of injury to plant tissues, associated with the feeding punctures of many species of plant bug, has been recognized for many years The injury generally has been attributed to the toxic effect of the salivary secretions of the insect, but more recent investigations have shown that, in many cases, it is caused by microorganisms introduced into the plant tissues by the insects while feeding

Nowell (1917*a*, 1917*b*, 1918) apparently was the first to point out the true nature of the injury associated with the feeding punctures of certain of these insects   He investigated the internal diseases of cotton bolls in the West Indies and showed that the staining of the lint was caused by four yeastlike fungi, the most important of which were two species of *Nematospora* These fungi were found abundantly internally, in immature unopened bolls on which there was no visible surface infection The disease was produced experimentally by subjecting healthy bolls to the feeding of two genera of plant bug, the cotton stainers *(Dysdercus spp)* and the green bug *(Nezara viridula* L) Two other insects [*Leptoglossus bolteatus* and *Phthia picta* (Drury)] were incriminated but were considered of less importance than the first two   No other natural method of inoculation was found   When very young bolls are fed upon, they drop off, older ones remain attached, but the lint is stained   Stringent efforts to control the bugs resulted in fair control of the disease

The nature of the association of the fungi with the beetles was not determined by Nowell   There is some evidence that there are some individual bugs which do not introduce the fungi when feeding   A slight proliferation of the tissues about the point of puncture is the only visible effect of the feeding of such insects   The way in which the fungi survive the winter, the source of contamination of the insects, and the extent of the association in the various stages of the life history of the insects were not determined

The life history and habits of the principal plant bugs that are injurious to cotton bolls have been described by Morrill (1910). The cotton stainers oviposit in the soil, and the eggs hatch in

about 8 days   There are five nymphal instars, all of which are capable of transmitting the fungi   From 45 to 50 days is required for the completion of the cycle

The fungi of stigmatomycosis were studied in more detail by Ashby and Nowell (1926), who identified four species (*Spermophthora gossypii* A   and N , *Eremothecium cymbalariae* Borzi, *Nematospora gossypii* A   and N , and *N   coryli* Peglion)   Of these, *N   gossypii* and *N   coryli* were most commonly associated with the disease of cotton bolls   These workers were the first to apply the term "stigmatomycosis" to the disease

The work of Nowell, who demonstrated that the disease was caused by fungi transmitted by plant bugs, was soon verified and extended by several workers in different parts of the world Laycock (1925) demonstrated the association of *D   superstitiosus* and other species of plant bug with *N   gossypii* in the production of the disease in Nigeria   Rhind (1927) found the disease in Burma, caused by *N   gossypii* and *N   coryli* to be disseminated by *D   cingulatus* A   Hansford (1930) proved that *N   gossypii* was disseminated and introduced into cotton bolls by *Dysdercus spp* in Uganda and pointed out that the young nymphs were not able to transmit the fungi into the bolls   Moore (1930) reported similar relationships in South Africa between *N gossypii* and *N   coryli* and *D   fasciatus* and *D   nigrofasciatus* The fungi were found also in spots on several kinds of beans as well as other plants fed upon by the insects   Steyaert (1934) described essentially the same relationship in the Belgian Congo, and Pearson (1934) reported extensive studies in the Transvaal and added *D   intermedius* as a vector   Important contributions to the study of stigmatomycosis in South Africa have been made by Ullyett (1930)

The relationship of fungi to the injury to cotton associated with the feeding of Hemipterous insects has received very little attention in the United States   Cassidy and Barber (1939), however, have called attention to the injury caused to cotton by these insects in Arizona where they estimate an average loss of five dollars per bale   Fifteen different species of Hemiptera were found to feed and breed on cotton, but most of the injury was caused by eight species, the most important of which were three Pentatomidae, namely, *Euschistus impictiventris* Stal , *Chlorochroa sayi* Stal , and *Thyanta custator* (F)   In discussing

the nature of the injury these authors state, "The most con-
spicuous injury, and the damage most keenly realized by cotton
growers, consists of the puncturing of the bolls, followed by the
development of severe lint staining by introduced pathogenic
organisms"

Wingard (1922) described from Virginia a "yeast spot" of
lima beans and cowpeas caused by *N phaseoli* Wingard and in
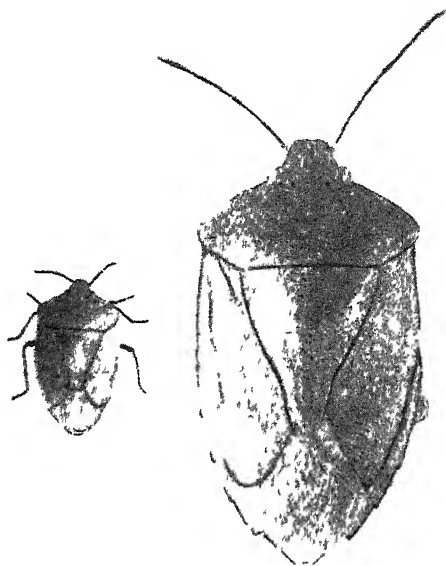
FIG 122 —The green stinkbug (*Nezara hilaris* Say), the vector of stigmatomy-
cosis or yeast spot of lima beans, natural size and approx 4× (*After Underhill*)

1925 reported proof of its dissemination by the green stink-
bug (*Nezara hilaris* Say) (Fig 122)   The bugs feed upon the
pods, their beaks penetrating the young seed   Brown, sunken,
necrotic lesions are formed on the seed (Fig 123)   Usually
only the seeds are affected, but when the bugs feed on very
young pods the necrosis is more general, and the entire pod
shrivels and falls off (Fig 124)   The life history of the bug
and a good description of the injury caused are given by Under-
hill (1934)   Wingard failed to isolate the pathogen from the
bug but claimed that failure was due to faulty technique   No

study was made of the source of contamination of the bugs or the method of survival of the fungus over winter

The bugs hibernate as adults under leaves and grass on the ground   They become active in late June and begin oviposition Eggs are deposited on the surface of leaves, fruits, or limbs of certain preferred wild hosts, especially American elder (*Sambucus canadensis* L), black locust (*Robinia pseudoacacia* L), and honey locust (*Gleditschia triacanthus* L)   Oviposition may continue throughout the summer, reaching a peak in the middle of July   The eggs hatch in about eight days   There are five

Fig 123 —Three lima-bean seeds showing the brown necrotic lesions caused by the yeast (*Nematospora phaseoli*) inoculated through the pods by the green stinkbug (*Nezara hilaris*)   (*After Underhill*)

nymphal instars requiring about five weeks for complete development   There is only one brood each season   The disease apparently may be transmitted by any stage of the insect although the information on this point is not complete

Beans are not the preferred host of the insects, they usually migrate to beans from the preferred wild hosts   The black locust, red bud, and linden trees are the most important in this respect, and it is recommended that beans should not be planted less than 100 yards distant from these trees   If practical, such trees should be removed

Lee (1924) and Fawcett (1929) have described a disease of citrus fruits caused by *N coryli* which they call "inspissosis" or "dry rot "   Fawcett (1929) showed that the pathogen was transmitted from pomegranates to citrus fruits by the leaf-footed plant bug [*Leptoglossum zonatus* (Dall)]   The disease

was experimentally transmitted by placing the insects, taken from infected pomegranates, on sound oranges and lemons in jars in the laboratory   The fungus was readily isolated from fruits inoculated by the bugs in this way   Attempts to isolate the fungus from the beaks of several individual bugs were not successful   Weber (1933*a*) has reported *N coryli* and *N gossypii* from citrus and several other different fruits in Florida
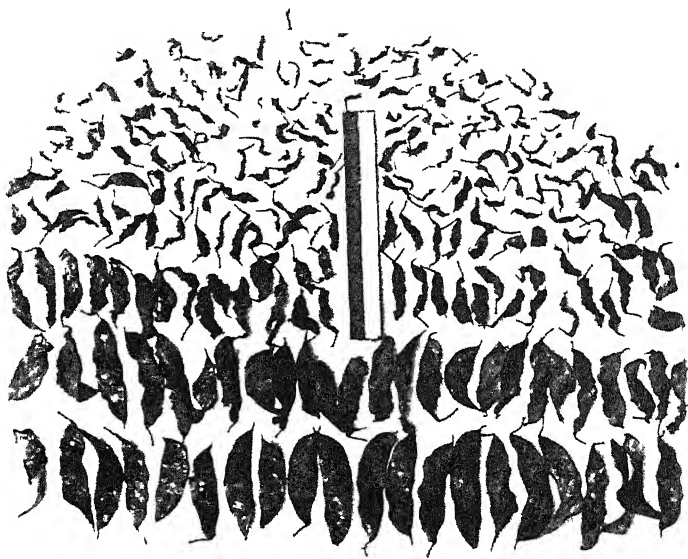
Fig 124 —Lima-bean pods shed from a single vine as a result of yeast transmitted by the green stinkbug   (*After Underhill*)

Stigmatomycosis, in some form, probably occurs on all plants on which the vectors feed

Weber (1933*b*) has described a kernel spot of pecan caused by *N coryli* and has observed its association with the feeding punctures of *Nezara viridula*   This was later verified by Demaree (1922) who suggested that "the pathological result may be caused by the mechanical rupturing of the host cells by the sucking up of the plant juices, by the injection of toxic substances into the tissues, or by the combined result of all three types of injury " In view of the described associations between the plant bugs and *Nematospora* throughout the world, it is quite probable that

kernel spot of pecans is a stigmatomycosis, in all respects similar to that on other plants and that *Nezara viridula* is the principal vector. Complete experimental proof, however, has never been established.

Wallace (1932) described a similar disease on the coffee bean which he showed was caused by *N. gossypii* and *N. coryli*. The fungi in this case were transmitted by the bug *Antestia lineaticollis*.

When one considers the injuries caused on many cultivated plants by plant bugs of this type, it seems probable that much of the injury may be due to fungi introduced by the bugs while feeding. The universal association of species of *Nematospora* with the insects in such widespread regions of the world would suggest that the association is more than a casual one. A thorough study of the possible symbiotic relationships between insect and fungus should be made. It is significant that no satisfactory explanation of the method of survival of the fungi over winter has been offered by any workers on the disease. The question of whether the fungus is constantly associated with the insects throughout their life history or whether they pick it up from some unknown source has never been answered. The problem of stigmatomycosis is in need of much more investigation.

The Anther Smut of Pinks —The better known smut diseases affect members of the grass family, all of which are wind-pollinated. Those smuts which infect grasses through the floral organs usually form spores at flowering time which, like the pollen grains, are dependent upon wind for their dissemination. There are a few smuts that infect through the floral organs of insect-pollinated plants. In these cases, the smut spores are specially adapted to insect transmission. The anther smut of pinks (*Caryophyllaceae*), caused by *Ustilago violaceae*, is the best known example of the insect-transmitted smuts. The phenomena of infection in *U. violaceae* have been described by Brefeld and Falck (1905).

The spores of the fungus are formed in the anthers of infected plants, where they replace the normal pollen grains. The fungus infection is systemic, and although all flowers on an infected plant are usually smutted, the spores are formed only in the anthers. The spores are approximately the same size as the pollen grains, but darker in color. They are, like the pollen grains, somewhat

sticky and are not easily scattered by the wind   The flowers of
the host plant open in the evening and remain open after dark
Pollination is brought about by several species of sphinx moth
that visit the flowers in search of nectar   When an infected
flower is visited, the insect becomes contaminated with the smut
spores, which it transmits eventually to the stigmatic surface of a
healthy flower   The spores find the stigmatic secretions a favor-
able medium for germination and growth   The infecting
mycelium penetrates the young ovary but does not destroy it
When the seeds from such infected flowers are planted, they
produce systemically infected plants, all the flowers of which
produce only smutted anthers

This disease is a striking illustration of the adaptation of a
fungus to insect transmission   The association is probably a
very old one and may have evolved along with the host and its
adaptation for insect pollination

Blossom Blight of Red Clover —This disease, caused by
Botrytis anthophila Bond , was first observed in Russia by
Bondarzew (1913)   It has been observed more recently in Wales
and has been described in some detail by Silow (1933)   The
fungus fruits on the anthers of affected plants where the yellow
pollen grains are destroyed and replaced by gray spores of the
fungus (Fig 125)   Usually, all the florets on the clover head are
affected, but occasionally some normal anthers are produced
The vigor of the plant is not impaired, the blighted anthers con-
stituting the only visible symptoms   The greatest economic
importance of the disease results from the decreased yield of seed

Bondarzew (1914) observed bees visiting infected florets and
suggested that they were vectors of the disease   Similar observa-
tions were made by Silow, who demonstrated experimentally that
bees were the principal vectors   Red clover is largely dependent
upon bees for pollination, and the bees, in searching for nectar
in infected flowers, become contaminated with spores, transmit-
ting them to the stigmatic surfaces of healthy flowers   The
spores germinate and penetrate the style (Fig 125c), the
mycelium eventually reaching the ovary   The ovary is not
destroyed but develops normally   The mycelium, however,
persists under the seed coat (Fig 125d), where it remains dormant
until the seed sprouts   When the seed germinates, the mycelium
begins to grow and systemically infects the young plant   The

growth of the fungus keeps pace with the plant, and when flowers are produced on the new plant, the mycelium penetrates the anthers and sporulates (Figs 125*a* and *b*)

The transmission of anther blight by bees closely parallels the transmission of anther smut of pinks by the sphinx moth, and both associations resemble very much the better known phenomena of insect pollination   The life habits and methods of fructification of both pathogens are obviously adaptations for insect transmission

FIG 125 —*Botrytis anthophila*   *a*, a blighted anther on which the fungus is fruiting, *b*, an enlarged sporophore showing how the spores are borne, *c*, a stigma of a clover blossom showing pollen grains and Botrytis spores germinating and penetrating the style, *d*, a section through the seed coat of a clover seed showing the mycelium of the fungus   (*After Silow*)

Tree-cricket Canker of Apple —Parrot, Gloyer, and Fulton (1915) and Gloyer and Fulton (1916) described a canker of apple trees that was associated with the oviposition punctures of tree crickets (Fig 126)   They showed by experiments that the cankers were caused by *Leptosphaeria coniothyrium* (Fckl) Sacc and that the disease was transmitted by tree crickets   They called the canker "tree-cricket canker " The fungus causes also a cane blight of raspberry that is often transmitted by the same insects   In the course of the study of transmission of this

cankei disease, it was found that the tiee ciickets disseminate other species of fungi and that they aie piobably conceined in the spiead of seveial diseases
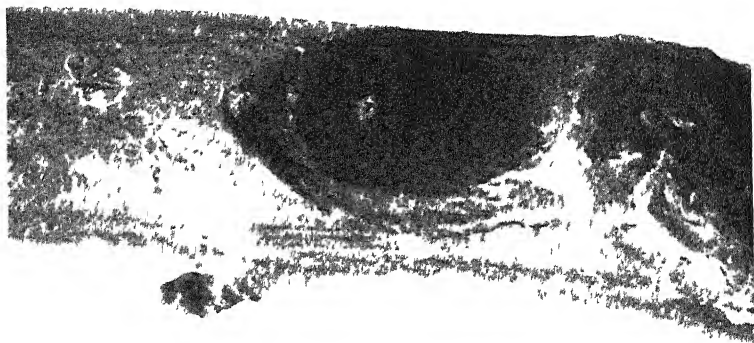
Fig 126 —A typical tree-cricket cankei on an apple branch   The light spot in the center is the oviposition puncture wheie infection took place   (*Afte1 Gloyer and Fulton*)
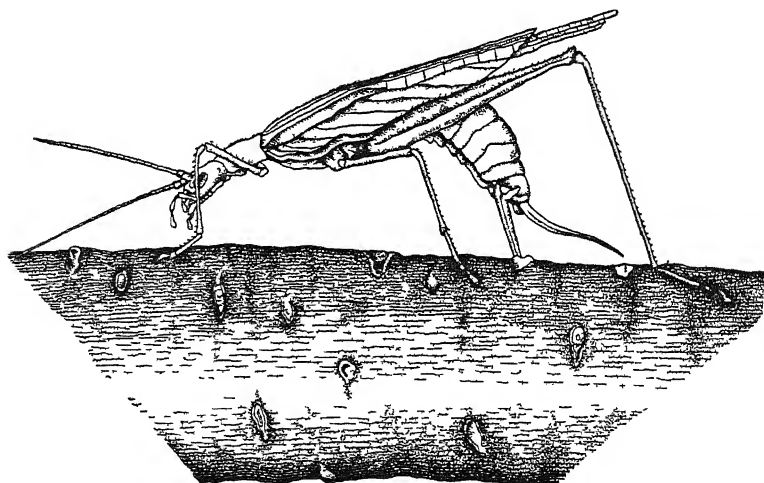
Fig 127 —A tree cricket (*Oecanthus niveus*) in the act of oviposition   (*Redrawn after Parrot and Fulton*)

In order to undeistand cleaily how the tiee ciickets transmit the disease, it is necessary to know something of the life history and habits of the insects   A good description is given by Paiiot

and Fulton (1914)   The role of two species as vectors was studied extensively by Gloyer and Fulton (1916)   These were *Oecanthus niveus* De G , the snowy tree cricket, and *O angustipennis* Fitch, the narrow-winged tree cricket, the most prevalent species on apples in New York   In late summer, these insects oviposit in branches and twigs of apple trees   *O niveus* oviposits chiefly in branches 1 to 2 inches in diameter while *O angustipennis* selects smaller branches ranging from ⅓ to ½ inch in diameter   The female first chews a hole in the outer bark, then inserts her ovipositor, deepens the hole, and deposits an egg (Fig
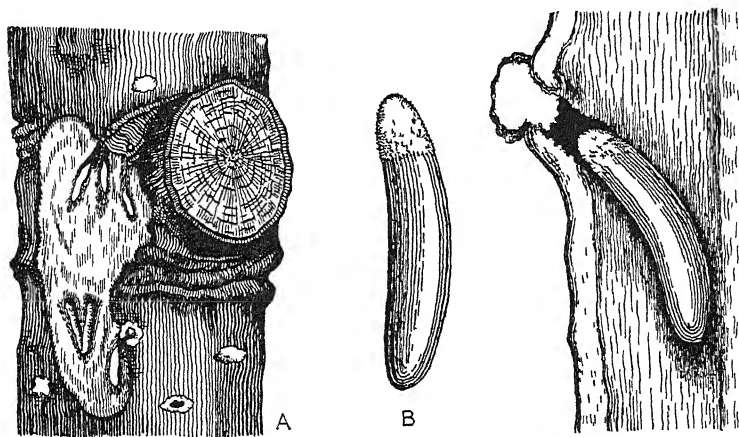
Fig 128 —The method of oviposition of the snowy tree cricket   *A*, an apple twig with a portion of the bark removed to show egg punctures (approx 1½ ×)   *B* an egg (approx 20 ×)   *C*, a section through an egg puncture showing egg in place and the plug of feces with which the hole is closed (approx 16 ×)   (*After Parrot and Fulton*)

127)   A drop of mucilaginous fluid is secreted on top of the egg   *O niveus* covers the egg and plugs the hole with a pellet of feces, and *O angustipennis* uses a pellet of chewed bark, usually taken from diseased tissue (Fig 128)

Tree crickets are omnivorous feeders, eating any organic material of sufficient softness, including soft insects such as aphids and scale insects   They also feed on decaying plant tissue and the associated fungus spores and mycelium   Microscopic examination of adult tree crickets shows abundant spores of many fungi on all parts of the body   Viable spores of many species of fungus, including *L coniothyrium*, are found abundantly in the intestinal tracts and in fecal pellets   From these facts, it is evident that the

act of oviposition is an effective means of inoculating the apple twigs with the pathogenic fungus   Not all oviposition punctures result in cankers, but enough of them are infected to make the insect a vector of major importance   The eggs do not hatch until June of the year following oviposition, and there is only one brood in the region of New York

Because of the omnivorous feeding habits of the insects and their preference for soft decayed tissues, it is probable that they are to some extent vectors of other diseases   Garman in Kentucky, as early as 1904, reported brown rot of peaches developing from the feeding wounds of tree crickets on peaches and plums and black rot from feeding wounds on grapes   Urbahns (1923), also, reported destructive outbreaks of brown rot in California following the feeding punctures of these insects   Both the feeding and breeding habits of the tree crickets make them potential vectors for many plant diseases   They should be looked upon with suspicion when they are found associated with almost any plant disease

Chestnut Blight —The *Endothia* canker of chestnut, or chestnut blight, was first discovered in one of the parks of New York, in 1904, presumably having been introduced from the Orient on imported Japanese chestnut trees   It is caused by *Endothia parasitica* (Murr) Anderson and Anderson, an Ascomycete of the order Sphaeriales   The fungus produces a rapidly developing canker of the twigs, branches, or trunk of the tree   Infection is usually fatal, leading to the death of the tree in a relatively short period of time   The chestnut-blight pathogen has been thoroughly described by Shear, Stevens, and Tiller (1917)   The disease has spread rapidly throughout the range of the chestnut in the eastern United States, in the course of less than 25 years after its discovery, it had destroyed almost the entire stand of native chestnuts in North America   A strenuous campaign was waged to eradicate and check the spread of the disease, but all efforts were in vain   It spread so rapidly that no practical means of checking it was ever discovered   In the course of this eradication campaign, it is only natural that considerable attention should have been given to the various methods of spore dissemination which enabled the disease to spread so quickly

From the very beginning of the study of the disease, insects were considered as important agents in disseminating the spores,

but the idea was based largely on observations and inference
Rankin (1912) stated that "reasoning by analogy with what is
known of the behavior of many fungi, such agencies as borers,
buds, ants, and the wind, etc, have been suggested but in no
wise proved to be responsible " The most extensive study of
insects as possible vectors of the disease was made by Studhalter
and Ruggles (1915) Heald, Gardner, and Studhalter (1915)
demonstrated that although the ascospores were readily dis-
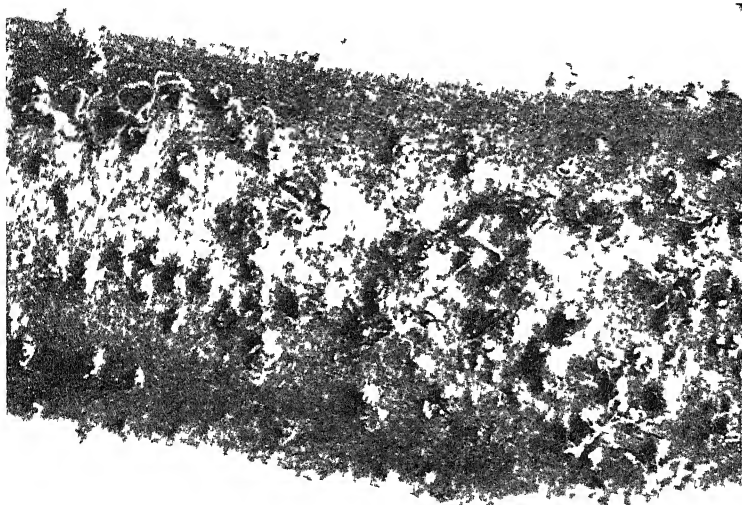
FIG 129 —A branch affected with chestnut canker showing the extrusion of
spores from the pycnidia in long sticky spore horns ' These spores adhere
readily to insects and birds and may be carried for long distances by them
Local dissemination is accomplished most readily through rain water   (*After
Heald*)

seminated by wind, the pycnidiospores were not so well adapted
to wind dissemination, being extruded in long, sticky spore horns
that become hard on drying (Fig 129)   The spores were shown
to be better adapted to dissemination by water and insects
Studhalter and Ruggles studied the spores found on about
seventy-five individual insects representing about twenty-five
different species, all taken from chestnut-blight cankers   They
found that about 30 per cent of them carried spores on their
bodies, and they concluded that the insects were of importance as
vectors of the disease

The conclusions of Studhalter and Ruggles, however, were strongly criticized by Craighead (1916), who pointed out that most of the insects on which spores were found rarely visited or attacked living trees and for this reason could be of little significance as vectors of chestnut blight   He maintained that other insects not studied by Studhalter and Ruggles would be more likely to transmit the disease   The most likely insect vector according to Craighead is the long-horned beetle (*Leptura nitens* Forster) which bores in the bark of over 90 per cent of the living chestnuts over 10 inches in diameter   He states that this species has adapted itself to breeding in great numbers in chestnut-bark cankers, a fact which suggests strongly that it is an important vector   It is to be regretted that this insect was not studied more thoroughly

Craighead claimed that the beetle *Leptostylus macula* Say, considered by Studhalter and Ruggles as the most important vector, rarely ever visited living trees and could not be of significance in transmitting the disease to healthy trees   On the other hand, Craighead (1912) believes that this insect, by eating the spores and preventing their dissemination, retards rather than aids the disease in its spread   *Leptostylus macula* may be of no significance as a vector, but it is difficult to believe that the quantity of spores eaten by the insect would be a significant check to the spread of the disease   Craighead recognized the possible importance of many species of insects in making fresh wounds through which spores disseminated by wind could infect   He states that such wounds have been found infected and expresses the belief that the making of wounds, through which wind-blown spores infect, is the chief role of insects in the epiphytology of chestnut blight

Chestnut blight spread so quickly over the entire range of the chestnut, as stated above, that all efforts to control it were discontinued   Thus, interest in the study of the method of its spread also waned, and the problem of insect transmission of the disease was left only partly solved

Heald and Studhalter (1914) demonstrated that several species of bird were also vectors of the chestnut-blight pathogen, suggesting that migratory species could be responsible for long-distance dissemination and new centers of infection   The fungus is well adapted to rapid dissemination by birds and many other agencies,

but the relative importance of the different agencies of dissemination has never been determined   For a more detailed discussion of the role of birds as vectors of chestnut blight, see Chap XI

Insects and Tomato Leaf-spot Diseases —Martin (1918) has investigated the role of several leaf-eating insects in the dissemination of spores of *Septoria lycopersici* Speg and *Alternaria solani* (E and M) Jones and Grout, causing leaf spots of tomato   It was first observed that flea beetle punctures frequently formed the center of an early blight infection   Flea beetles (*Epitrix cucumeris* Harris) collected at random in tomato fields were found to carry viable spores both externally and in their intestinal tracts   It was demonstrated that the spores of both fungi pass through the alimentary canal and survive uninjured in fecal deposits   Similar relationships were demonstrated for the Colorado potato beetle (*Leptinotarsa decimlineata* Say) and the tomato worm (*Protoparce carolina* L)

Unfortunately, neither disease was experimentally transmitted by the insects concerned   The conclusion that they serve as vectors is based on circumstantial evidence only

It was further shown that pickers carry great quantities of spores on their hands and garments, and Martin concludes that much of the inoculum is disseminated in this way   Pickers are considered to be of more importance than the insects, which are of greatest importance in the dissemination of inoculum early in the season

Insects and Sooty Mold —Many crop plants, especially those of tropical or subtropical regions, are often severely affected with a disease known as "sooty mold," caused by a number of different species of fungi possessing dark-colored mycelium   One of the most common of the sooty mold fungi is *Capnodium citri* which causes the troublesome sooty mold of citrus fruits   The fungi grow as black velvety membranes over the surfaces of leaves and fruit (Fig 130)   They are not true parasites, for they do not penetrate the cells of the plant but live entirely on the surface and derive their nourishment from honeydew secreted by insects   Even though the sooty mold does not parasitize the plant, it severely injures the tree by forming a mat of black mycelium that covers a large proportion of the leaf surface and thus interferes with the processes of photosynthesis and respiration   This results in lower yields of poor-quality

fruit and makes the trees less resistant to drought or other adverse factors   The fungus also may disfigure the fruit and appreciably reduce its market value   Any insect that secretes honeydew in sufficient quantity may meet the requirement of the sooty-mold fungus   Scale insects, aphids, and the larvae of white flies are most frequently associated with sooty molds

One of the best descriptions of the association has been given by Webber (1897), who described in detail the sooty mold of orange in Florida   Here the fungus was associated with the white fly (*Aleyrodes citri* R and H), the wax scale (*Ceroplastes floridensis* Comstock), several species of *Lecanium*, the mealy bug (*Dacty-*
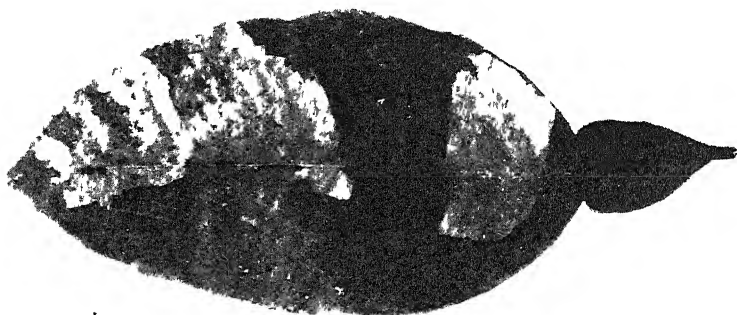
FIG 130 —A citrus leaf affected with sooty mold   Some of the mold has been
stripped off exposing the leaf surface   (*After Rhoads*)

lodius citri Risso), and the aphid (*Aphis gossypii* Glov)   Of these insects, the white fly (*A citri*) was by far the most important

The insects for the most part feed upon the lower surfaces of the leaves   The honeydew secreted by them falls principally on the upper surface of the leaves and fruit immediately underneath, and it is here that the sooty mold grows most luxuriantly Several different kinds of spore are formed by the sooty-mold fungi, most of which are readily disseminated by wind   There is no evidence that they are disseminated more than incidentally by the insects furnishing the honeydew on which they grow

Because the black mold is dependent upon the insects for its nourishment, the most effective means of control has been indirectly through the control of the insects   This has been

accomplished by spraying with insecticides, by fumigation with hydrocyanic acid gas, and by the use of natural enemies such as entomogenous fungi and insect parasites. Practical experience has shown that when the insects are destroyed the sooty-mold fungi disappear, thus confirming the dependence of the fungi upon the insects for nourishment.

Insects and Brown Rot of Stone Fruits —Brown rot caused by *Sclerotinia spp* is one of the most destructive diseases of stone fruits, causing enormous losses by decay of the fruit as well as through blossom and twig blight. The disease is almost world-wide in its distribution, and there are few places where peaches can be grown successfully without spraying to control the rot.

The spores of the brown-rot fungus are commonly wind-borne, and although the pathogen may penetrate the skin of uninjured fruits through stomata and lenticels, infection is facilitated by wounds. The feeding and oviposition wounds made in the fruit by the plum curculio (*Conotrachelus nenuphar* Herbst) are very frequently portals of entry for the fungus (Scott and Quaintance 1911). It is generally assumed that wind-blown spores are responsible for the infection that takes place through the insect punctures, but as the curculios have abundant opportunity of becoming surface-contaminated with spores it is very probable that they also disseminate the spores and introduce some of them into the freshly made wounds.

The significance of the curculio as a vector of brown rot is more evident in orchards sprayed with lime sulphur where infection by wind-blown spores is reduced to a minimum. In one experiment reported by Scott and Ayres (1910), 93 per cent of the fruit infection could be traced to curculio wounds.

In view of the importance of the curculio in brown-rot infection, it is obvious that a sound control program for brown rot must include provisions for the control of the curculio.

The Potato Flea Beetle and Potato Scab —Scab caused by *Actinomyces scabies* (Thaxter) Gussow is one of the most prevalent diseases of the potato. The pathogen lives indefinitely in the soil and infects the developing tubers, causing the well-known corky scab pustules. Ingression is chiefly through the lenticels, but wounds also may serve as infection courts.

MacMillan and Schaal (1929) have demonstrated that the scab pathogen commonly infects the tissues injured by the larvae

of the potato flea beetle (*Epitrix cucumeris* Harris)   In the absence of scab, the injury caused by the flea-beetle larvae consists of inconspicuous "worm tracks" with a smooth surface, differing only in color from the normal periderm   When infected by scab, the worm tracks are raised, bulging, and eruptive, seriously decreasing the market value of the tubers   In other cases, the lesions caused by the flea beetles are invaded by *Rhizoctonia solani*, a fungus that usually does not infect the tissues of the tuber

Schaal (1934) investigated further the association of scab with flea-beetle injury and has demonstrated that flea-beetle larvae, collected from potato soil, carry *Actinomyces* both externally and internally   The pathogen was not found in or on the eggs of the beetles when deposited in sterilized cages The insect in all probability plays no part in the dissemination of the pathogen but is an effective agent of inoculation, a large part of the injury being caused by the scab pathogen that it introduces

Blackleg of Cabbage and the Cabbage Maggot —Blackleg of cabbage and other crucifers is caused by a fungus [*Phoma lingam* (Tode) Desmaz]   It causes a dry, black necrosis of the roots and stem, often killing the plant in relatively early stages of development   It also may cause a spotting of the leaves and a decay of the cabbage head in storage   The disease was first studied extensively by Ritzema Bos (1906) and Quanjer (1907) in Holland   Quanjer concluded that the fungus could not infect the roots unless they were injured and that the injuries made by the cabbage maggot (*Hylemyia brassicae* Bouche) were the principal avenues of entrance   His belief that the fungus was not seed-transmitted caused him to place special emphasis on maggot infestation as a prerequisite for infection   Henderson (1918), however, has shown that the fungus is readily seed-transmitted and the roots and stems may be infected without previous injury   These results naturally raise the question of the importance of maggot infestation in the epiphytology of the disease   Unfortunately, Henderson did not investigate this aspect of the disease extensively   Even though the maggot injury may not be necessary, Quanjer's observations indicate that it may be a significant contributory factor   There is need for a more careful study of the relationship of insect injury to

blackleg infection and development in light of the more recent information about the parasitism of the fungus

Insects and the Red Rot of Sugar Cane —Red rot, caused by *Colletotrichum falcatum* Went, is one of the most destructive diseases of sugar cane in the United States   It causes severe rotting of the stalks, stubble rhizomes, and leaf mid-ribs   It has been the cause of failure of a number of the leading commercial varieties of sugar cane   A complete account of the disease in Louisiana and Florida has been published by Abbott (1938)

Red rot is transmitted in several different ways   Spores are produced abundantly and are widely disseminated by the wind   Although infection may occur by direct penetration of the epidermis, the most destructive phases of the disease are those following infection through wounds   According to Abbott, infection of the stalk, in Louisiana and Florida, occurs principally through the tunnels of the moth borer (*Diatroea saccharalis* F)   Injuries made by the sugar-cane weevil (*Anacentrus sp*) also may serve as points of infection for underground parts of the stalk   Abbott concludes that infection of the leaves occurs most frequently through insect wounds, although direct penetration of uninjured epidermis is recognized   No studies of the detailed relationships between the insects and the fungus have been reported   One would assume from much of the published statements that infection is accomplished by wind-blown spores which enter the wounds made by the insects, but in all probability careful study would show that the spores are introduced by the insects in their feeding activities

Insects and Diseases of Mushrooms —Cultivated mushrooms are subject to a number of destructive diseases, several of which are transmitted extensively by insects   The most important of these are "bubbles" and "plaster mold "   The former is caused by a fungus (*Mycogone sp*) that greatly distorts the mushroom, causing it eventually to become soft and decayed   Plaster mold is caused by a fungus that does not parasitize the mushroom directly but grows throughout the compost and prevents the normal development of the fruiting bodies   According to Charles and Popenoe (1930), spores of both these fungi are disseminated by the various species of fungus fly that infest the mushroom   Charles states

In houses where these diseases occur mushroom flies have been examined which carried on their somewhat spiney bodies and legs hundreds of spores of these fungi   These flies move actively about through mushroom houses, both by walking and by flight, and are undoubtedly responsible for the rapid increase in the distribution of the diseases in large houses   Diseased mushrooms develop an odor likely to attract some of the larger carrion flies from the outside and these larger flies are capable of carrying much greater numbers of spores throughout the house

The control of both diseases is aided by adequate control of the insect vector

Plum Wilt and the Peach-tree Borer —Plum wilt, a destructive disease of plum trees in Georgia, was described in 1916 by Higgins, who concluded that wounds made by the peach-tree borer (*Aegeria exitosa* Say) were the most important avenues of infection   Plum wilt is caused by the fungus *Lasiodiplodia triflorae* Higgins, which is a vascular parasite affecting principally the conducting elements and the medullary rays in the wood   The wilting results from the inhibition of the water movement by gum deposits

The fungus cannot penetrate the uninjured bark and is entirely dependent upon wounds   Although mechanical injuries and wounds made by other agencies may serve as portals of entry, the wounds made by the borer appear to be of greatest importance

The disease is more destructive on the Japanese plums and hybrid varieties of Japanese-plum parentage   One of the reasons for this varietal preference was attributed by Higgins to the use of peach stock on which to bud the plums   The peach stock is more attractive to the borer than plum wood, and infestation that takes place in the peach stock spreads readily into the plum wood

The fungus fruits on affected trees near the surface of the soil where the bark is continually moist, and the spores are extruded from the pycnidia in white masses or in long gelatinous tendrils   The method of dissemination of the spores is not fully known, and the question of whether or not the spores are disseminated by the adult borer has been left unanswered

The peach-tree borers are Lepidopterous insects   They hibernate in the soil or in the bark of infested tree trunks in the pupal stages, emerging as adult moths in early spring   Eggs

are deposited on the surface of the bark of Drupaceous trees near the base of the trunk   The young larvae bore through the bark soon after hatching and complete their development in the inner bark of the roots or the base of the trunk   Although many varieties of Drupaceous tree are attacked, the borer is primarily a pest of the peach or of trees grafted on peach stock

Insect Dissemination of the Cotton-wilt Pathogen —Fusarium wilt caused by *Fusarium vasinfectum* Atk is a destructive disease of cotton throughout the southern part of the United States   In common with other pathogens of this kind, it spreads relatively slowly through the soil   The appearance of the disease in new localities in small areas in the field is not uncommon, indicating that aerial dissemination of inoculum occurs in some way   It is not always possible to determine the origin of these local infestations, and the method of aerial dissemination has been a subject of much speculation   Taubenhaus and Christensen (1936) have investigated the survival of *F vasinfectum* in the intestinal tract and fecal pellets of numerous insects that normally feed on cotton plants   The fungus was recovered in viable condition from the fecal pellets of nearly all the species tested, except those which feed normally on decaying organic matter (*Collembola*, etc)   The following grasshoppers were found to act as agents of dissemination of the fungus *Melanoplus differentialis* Thos , *M mexicanus* Sauss , *M femur-rubrum* De G , *Encoptolophus texensis* Brun , *Spharagemon cristatum* Scudd , *Tomonatus aztecus* Sauss , *Choriophaga viridifasciata* var *austrator* De G , *Schistocerca americana* Drury, *S obscura* Fabr , *Trimenthopis citrina* Scudd , and *Dissosteira carolina* L   These insects were considered of importance in field-to-field spread of the disease   All evidence indicated that the association between insect and fungus is entirely mechanical and that the passage of the fungus through the alimentary tract in the form of spores and mycelial fragments is relatively rapid

Monochamus spp and Heart Rot of Conifers —The relationship of wood-boring beetles and wood decay in logs of red pine has been studied by Leach, Orr, and Christensen (1937)   When freshly cut logs were exposed to insect infestation, bark beetles were the first insects to attack them   The bark beetles were soon followed by various other insects, including several wood-boring species   As soon as the logs became infested with insects,

the sapwood was rapidly decayed by fungi   The most prevalent
fungus was *Peniophora gigantea* (Fi) Massee, which eventually
spread to the heartwood, causing a reddish brown decay   It was
demonstrated that there was a definite correlation between the
amount and rapidity of heartwood decay and the infestation by
Monochamus scutellatus (Say) and *M notatus* (Drury)   All
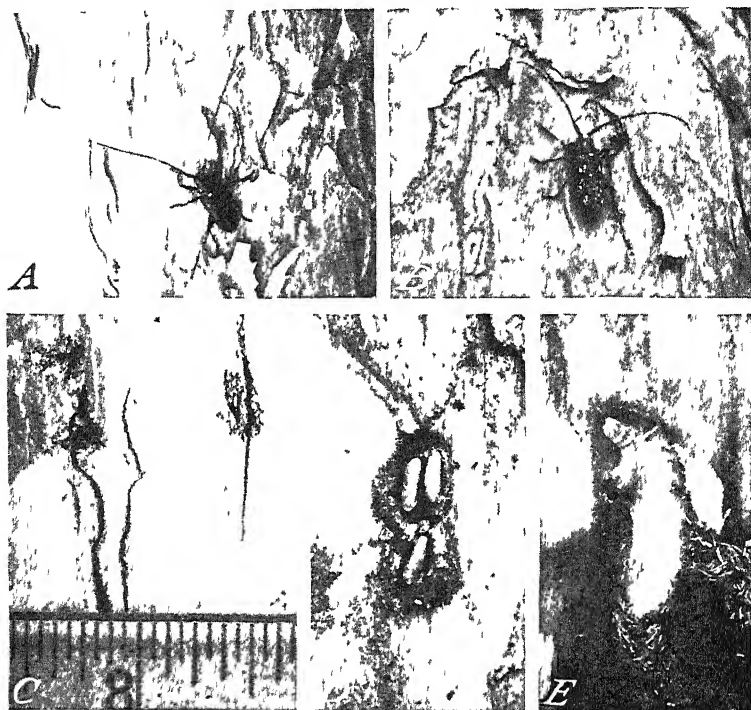
Fig 131 —*Monochamus scutellatus*, a wood boring insect that aids a wood-
rotting fungus in the invasion of the heart rot of conifers   *a* a male, *b*, a female
cutting an egg niche through the bark, *C*, egg niches, *D*, eggs in the inner bark,
E, a larva feeding on the inner bark and outer sapwood

evidence indicated that the beetles were not responsible for
introducing the fungus into the log but that they aided the fungus
in the invasion of the heartwood and so hastened its destruction
    The beetles (Fig 131) lay their eggs in the inner bark through
niches made with their chewing mouth parts   On hatching, the
larvae feed for some time on the inner bark and outer layers of
sapwood where they become contaminated with the wood-rotting

fungus As the larvae approach maturity, they bore deep into the heartwood, later returning to the sapwood to pupate (Fig

FIG 132 —A section through a red-pine log showing the decay associated with the larval tunnel of *Monochamus scutellatus* in the heartwood The larva entered the wood through the ovoid hole at the left, and the mature beetle emerged from the round hole at the right
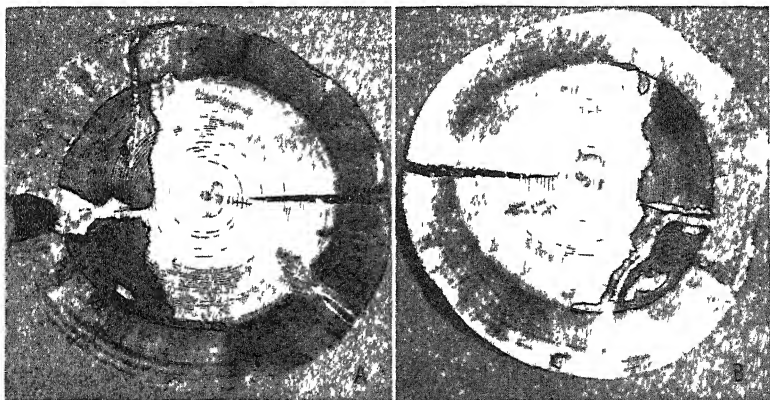
FIG 133 —Two sections of the same experimental red-pine log showing two areas of decay, each arising from a larval tunnel of *Monochamus scutellatus*

132) Observations on experimental logs showed that the greater part of the heartwood decay always spread from the larval tunnels (Figs 132 and 133)

The fungus spreads through the wood in a longitudinal direction much more rapidly than in a radial or tangential direction The larvae take the fungus deep into the wood radially and tangentially after which it spreads rapidly up and down the log

Several species of buprestid beetle also attack the logs, but they apparently do not influence greatly the development of heart rot   The larvae keep their tunnels packed with frass and do not move about in them   The *Monochamus* larvae, however, keep their tunnel open and move back and forth frequently in disposing
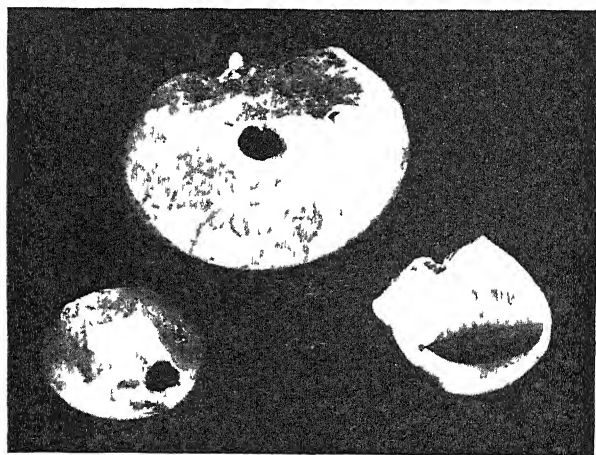
FIG 134 —Three fruiting bodies of *Polyporus volvatus*, showing the small opening through the membrane that encloses the hymenial layer forming a chamber in which the spores accumulate   The sporophore on the right has been cut in section in a vertical plane through the opening and shows the internal structure

of their frass   This difference in habits may explain in part the difference in their influence on the rate of decay

Insects and a Sapwood Decay of Conifers —The sapwood of trees of various coniferous species is sometimes decayed by *Polyporous volvatus* Pk   The decay affects dead or dying trees, especially those infested with bark beetles   The fruiting bodies nearly always grow out of the holes made through the bark by the beetles, and there is considerable evidence to show that the spores are introduced into the sapwood by the beetles (Hubbard 1892) The fruiting surface of the sporophore is at first completely covered with a leathery membrane continuous with the upper surface   As the sporophore matures, a small opening is formed in

the center of the membrane   The spores are shed within the cavity and are not subject to wind dispersal (Fig 134)   However, beetles and other insects enter the hole and, in crawling about within the enclosed space, become contaminated with the spores which they presumably introduce under the bark as they infest new trees   Hubbard has observed more than a dozen different species of insect in the spore chamber or feeding upon the sporophores   The bark beetles, because of their habit of boring into the bark, have the greatest opportunity of inoculating the sapwood and are generally considered to be the most important vectors

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CHAPTER VIII

INSECTS AND VIRUS DISEASES

The viruses that affect plants cause some of the most destructive diseases of agricultural crops. Early records reveal that virus diseases were prevalent on certain cultivated crops more than three hundred years ago, yet the full extent of the damage caused by them was not recognized until after the close of the last century. There is indeed much evidence for the view that the virus diseases as a group have become more prevalent and destructive in recent years. This may be explained to some extent by the more general recognition of virus diseases following the extensive study of the past 25 or 30 years. On the other hand, the great increase in commerce and travel and the exchange of plant materials would favor the spread of viruses to new regions. Moreover, it is a recognized fact that commerce has resulted in distributing many insect vectors to new regions throughout the world.

It must be recognized as a possibility also that viruses which originally affected only wild plants may have become more destructive to cultivated plants. An increasing amount of the land has been brought under cultivation with a corresponding destruction of the weed hosts of both the viruses and their insect vectors. It is only reasonable to suppose that as this change occurred the insect vectors and the viruses transmitted by them would become more prevalent on the cultivated crops. This is especially true of such viruses as curly top of sugar beet, aster yellows, and spotted wilt of tomato, each of which has a very wide host range among both weeds and cultivated plants.

A relatively large number of virus diseases of plants have been described in the past 25 years, and new ones are being reported at very frequent intervals. Extensive bibliographies on virus diseases have been published by Atanasoff (1934, 1937), Otero and Cook (1934, 1935, 1936), Cook (1935a, 1936a), and Smith (1937a). Cook (1935b, 1936b) has published, also, an extensive

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index of insect vectors of virus diseases   Almost all cultivated crops are affected by one or more viruses   At least 25 different viruses have been reported as affecting the potato (Folsom and Bonde 1936), and more than a dozen are known to attack tobacco It is probable that the same virus has been described under different names on different host plants   A single plant also may be affected with more than one virus, resulting in a confusion of symptoms that makes identification difficult   Many of the virus diseases, originally thought to be caused by a single virus, on further study have been found to be caused by two or more viruses that could be separated by appropriate methods   The number of viruses recognized as distinct are so numerous that no effort will be made here to discuss them all, not even all those known to be transmitted by insects   A relatively complete descriptive list of the known plant virus diseases has been published by Smith (1937a)

The identification of the various viruses is difficult because their true nature is still uncertain   For many years, plant pathologists have been inclined to accept the hypothesis that viruses are ultramicroscopic microorganisms living as obligate parasites   However, the more recent works of Vinson (1936), Vinson and Petre (1929, 1931), Stanley (1936a, b, c, 1937b, 1938a, 1938b), and others furnish evidence that the viruses may be inanimate and consist of proteins of high molecular weight which, in the presence of living cells, stimulate the production of more protein of the same kind   There are some objections to the concept of viruses as inanimate proteins, as pointed out by Rawlins and Takahashi (1938), Bawden and Pirie (1937), Gortner (1938), and others, yet the evidence is strongly in favor of the protein hypothesis   A final solution of this problem will greatly facilitate the study of virus diseases as well as their relationships with insect vectors

AGENTS OF VIRUS DISSEMINATION

No group of plant pathogens is more closely associated with insects than the viruses   There are very few, if any, true virus diseases that are not to some extent transmitted by insects, and there are many that are transmitted in nature only by insects Despite the importance of insects as vectors of virus diseases, there are several other ways in which viruses may be spread   In

many cases, a single virus may be transmitted by several different agencies, and the evaluation of the relative importance of each agent is an important factor in the control of virus diseases In addition to being transmitted by insects, virus diseases may be spread in nature by wind, water, seed, and vegetative propagation They may be transmitted artificially by inoculation and by grafting

Wind —Very important in disseminating fungus spores, wind is of relatively little significance in the spread of virus diseases Some viruses, however, such as that of tobacco mosaic are very resistant to desiccation and aging and may be disseminated by wind in the form of dried and crumbled leaf tissue Because the tobacco-mosaic virus infects so readily through the slightest injury, it is very likely that wind is of some importance as a vector, but, in general, dissemination in this way is relatively unimportant when compared with insect dissemination

A new virus disease of tobacco, tobacco necrosis (Nicotiana virus 11),[1] has been described by Smith (1937 c, d), who presented evidence to show that the virus is air borne Broad beans, which are also very susceptible to the virus, were infected when inoculated with previously sterile water through which air from the greenhouse containing infected tobacco plants was drawn Caldwell (1937) has objected to some of the conclusions reached by Smith, pointing out that the origin of the air-borne virus particles was not known and that infection by particles directly from the air had not been proved beyond question Price (1938) in an extensive study of this virus was unable to obtain any evidence that it was air borne No natural transmission was observed in his greenhouse experiments although old infected plants were present in the same house Smith, on the other hand, reported frequent and rapid spread which he interpreted as caused by air-borne particles of virus He concludes that the virus particles were washed into the soil, from which they gained entrance into the roots

Matsumoto (1938) reported another disease of tobacco and presented data that led him to believe that a virus was transmitted through the air directly from a diseased to a healthy plant In a footnote in a later paper, however, Matsumoto (1938) throws some doubt on the correctness of his earlier con-

[1] Classification of Kenneth M Smith

clusion by reporting the presence of some very small tyroglyphid mites on his experimental plants   It appears probable that he was not working with a true virus disease   The importance and significance of the problem of wind transmission justifies more extensive study under carefully controlled conditions, for if Smith's conclusions are proved correct, a new means of virus transmission will have been established   Extreme caution must be used, however, in drawing final conclusions   Every other possible means of transmission must be eliminated by rigidly controlled experiments   It would appear that a highly infectious virus could be readily transmitted by contact in handling the plants   These factors must be carefully controlled in experiments of this kind

Wind may be concerned also in so far as it may be a factor in the dissemination of the insect vectors   As pointed out in Chap XV, there is evidence that certain insects may be blown by wind for long distances   In general, however, it may be concluded that wind is a minor factor in the dissemination of viruses

Water —Water does not seem to be an important agent of virus dissemination   In violent wind and hail storms in which there is much wounding of tissue, wind and water combined theoretically could be responsible for much local spread of certain virus diseases   Moreover, when infection takes place underground, the soil water probably plays an important part in transmitting the virus   The significance of this type of spread is very difficult to evaluate, because it has not been the subject of much experimentation   Tobacco necrosis (Nicotiana virus 11), according to Smith (1937*b, c, d*), is readily transmitted by water to the roots, through which infection occurs without the aid of artificial wounding   This virus appears to be highly infectious and may be transmitted by contact, although it is difficult to transmit by grafting on most host plants

Guttation water apparently is of little significance in the transmission of viruses because, as shown by Caldwell (1930, 1931), viruses are rarely present in guttation drops even though the plant may be heavily infected   The virus apparently is unable to diffuse through the protoplasmic membrane into the tracheae Furthermore, when viruses are placed in the guttation drops, infection does not occur unless the adjacent plant cells are wounded

Soil —The term "soil transmission" is often used to denote a specific method of virus transmission, but there appears to be little or no justification for using the term in this sense   The soil is not an agent of dissemination, and the term merely covers a great amount of ignorance about the actual means of spread   Infection may take place through underground parts of a plant and be transmitted by insects working underground, by root contact, by soil water, or by direct inoculation through cultivation injury   Because of the difficulty of observing the underground plant parts, the actual mechanism of underground infection is usually obscure, but there is no reason for supposing that it is fundamentally different from infection through the aboveground parts of the plant

There is very little evidence to indicate that underground infection is common for many of the virus diseases   Webb (1927, 1928), however, has shown that in wheat mosaic infection may occur underground through either the roots or the crown, or both   Infection through parts of the plant aboveground apparently does not occur in nature   Wheat mosaic is transmissible by artificial sap inoculation, but no insect vector is known   The virus survives in the soil for an indefinite time and is not removed by thoroughly and repeatedly washing the soil   Neither the exact point of entrance through the roots or the crown nor the method by which entrance is accomplished is known   There is need for more thorough investigation of the ability of viruses to survive in the soil and the frequency of infection through roots and other underground parts of plants

Root infection of tobacco from contaminated soil has been reported by Lehman (1934) and by Johnson (1937), but the mechanism of infection was not determined   Smith (1937a, b) also has shown that tobacco plants may be infected through the roots by the virus of tobacco necrosis from contaminated soil water   However, the virus was not able to infect the roots of plants grown in water cultures contaminated with the virus   This fact would suggest the possibility that injuries caused by soil particles furnished the necessary wounds for infection   Evidence leading to the same conclusion has been presented also by Price (1938)

Seed —Seed transmission of viruses is known to occur, but it is not the rule   Perhaps the best-known and most striking case is

that of bean mosaic   Seed transmission of the bean-mosaic virus to the extent of 50 per cent has been obtained under experimental conditions   Seed transmission has been studied extensively by Nelson (1932) and Nelson and Down (1933), who have shown that seed infection of beans is very erratic, only a part of the seed on a badly diseased plant becoming infected   They have shown that often only a few seeds in a pod may transmit the virus and that the position in the pod is not the determining factor

Viruses appear to be more readily transmitted through the seeds of legumes than those of many other plants, but seed transmission is by no means confined to this family   Other examples have been reported by Doolittle and Gilbert (1919) in seed of wild cucumber, Kendrick (1934) in muskmelon seed, Elze (1931a) in potato seed, Newhall (1923) in lettuce seed, Berkeley and Madden (1932) and Doolittle and Beecher (1937) in tomato seed, and Henderson (1931) in petunia seed   For other examples of seed transmission of viruses, see the bibliography on seed-borne parasites by Orton (1931)

The factors governing seed infection are not very well known It is difficult to understand why it occurs in some plants and not in others and why only part of the seeds on heavily infected plants carry the virus   These occurrences would seem to indicate that the viruses are not so universally distributed in the tissues of the plants as has been generally believed

Pollen —Where seed transmission occurs, it has been assumed generally that the seeds become infected systemically from the infected mother plant   Another means of seed infection has been pointed out by Blakeslee (1921) who demonstrated that a virus on *Datura stramonium* is transmitted to the seed by pollen from infected plants in as high as 79 per cent of the seed   Reddick (1931) and Nelson and Down (1933) have shown that infected bean seed may be accounted for in this way   The possibilities of this method of transmission have not been extensively investigated   There is need for further work

Other Plant Parts.—Those plants which are vegetatively propagated provide one of the most effective means of virus dissemination and perpetuation   Recovery is rare in virus diseases of plants, and vegetative propagation from infected plants, whether by tubers, corms, cuttings, grafts, or any other method, usually results in 100 per cent infection of the progeny   Were it

not for the fact that many virus-infected plants yield progressively less until they fail to reproduce themselves and are eliminated, the percentage of infection in vegetatively propagated crops would eventually approach 100 per cent   This apparently is what has happened in the case of the latent virus of potatoes   Those varieties of potatoes in which the virus produces no ill effect, and consequently no tendency toward elimination of infected plants, have, in time, become universally infected

Parasitic Fungi —The possibility of virus transmission through the agency of parasitic fungi or bacteria has been suggested (Nelson 1932)   Theoretically it would be possible for spores of a parasitic fungus, produced on a virus-infected plant, to harbor the virus and introduce it into the cells of a healthy plant following germination and infection   This possibility appears remote, and no positive experimental evidence is available   Nelson (1932) observed that bean rust [*Uromyces appendiculatus* (Pers) Rev] taken from beans infected with mosaic did not transmit the virus when transferred to healthy plants

Man —Man himself is one of the most effective agents of virus dissemination   In the sale and distribution of seeds and plant parts and in pruning and other cultivating operations, viruses are disseminated widely   Valleau and Johnson (1927) have shown that tobacco mosaic may be spread by workers who chew or smoke tobacco while working with the tobacco plants   Many viruses are readily transmitted artificially by direct sap inoculation, but some are very difficult to transmit in this way   Still others have been artificially transmitted only by grafting   The majority of viruses are readily transmitted by grafting even though they may not be transmitted by other means

In a consideration of the transmission of virus diseases, there are a few fundamental facts that should be kept in mind   First, it should be remembered that there is no multiplication of the virus in the absence of living cells, in either plant or insect   Consequently it appears that the virus inoculum must come in contact with the protoplasm of the plant cell before infection occurs   This fact has led to the tacit assumption that some sort of wound is always necessary for virus infection   Sheffield (1936a), working with tobacco, tomato, *Nicotiana glutinosa*, and *Solanum nodiflorum*, presented evidence to show that tobacco-mosaic virus 1 and tobacco virus 6 cannot enter the

plant unless some of the surface cells are injured   Duggar and Johnson (1933), however, secured infection of tobacco plants by spraying the leaves with a suspension of tobacco mosaic virus   Since no wounds were made or could be detected, stomatal infection appears to be the only explanation   Drake *et al* (1934) and Sheffield (1936*b*) have emphasized the importance of plasmodesmata in infection and invasion of plant tissues by viruses   If virus particles entering through the stomata come in contact with plasmodesmata of the loosely arranged substomatal parenchyma, stomatal infection is more easily explained   Finally, one should bear in mind that there is much difference in the properties of different viruses, especially in regard to the influence of the extracellular environment   In all probability, there is as much variation among the plant viruses as there is among the plant pathogenic bacteria

Insects —Practically all the insect vectors of virus diseases are found in the following five orders

1 Orthoptera (grasshoppers)
2 Thysanoptera (thrips)
3 Homoptera (aphids, leaf hoppers, white flies, and scale insects)
4 Hemiptera (lace bugs and other plant bugs)
5 Coleoptera (beetles)

1 *Orthoptera* —The insects of this order all have chewing mouth parts, and they are as a rule not very effective as vectors of virus diseases   Spindle tuber of potatoes, a virus disease that is transmitted very easily by artificial inoculation, has been shown by Goss (1928, 1929, 1931) to be transmitted in nature by several species of grasshopper (*Melanoplus spp*)   The transmission apparently is entirely mechanical   Not many insects of this order have been incriminated as vectors of virus diseases

2 *Thysanoptera* —This order includes the thrips   These are small insects with asymmetrical mouth parts, and they feed with a rasping-sucking action   Thrips (*Frankliniella lycopersici* Andr and *Thrips tabaci* Lind) have been proved to be vectors of the spotted wilt of tomato, pineapple yellow spot, and a streak of peas (Samuel, Bald, and Pittman 1930, Linford 1931*a, b*, 1932)   These diseases eventually may be shown to be identical Transmission here is definitely biological and probably specific Although the ability of thrips to transmit other viruses has not been thoroughly investigated, it is probable that they may be

involved in the transmission of other virus diseases, where the relationship is less specific and the method of transmission purely mechanical However, because of the very shallow feeding wounds made by thrips, they would be of little importance as vectors of viruses that are localized in the phloem

3 *Homoptera*—This is by far the most important order of insects in regard to the transmission of virus diseases Approximately 90 per cent of all the insects concerned in the transmission of plant viruses are members of this order The vectors are found chiefly in the following families Aphididae (aphids, or plant lice), Cicadellidae (leaf hoppers), Fulgoridae (plant hoppers, or lantern flies), Aleyrodidae (white flies), and a few doubtful cases have been reported in the Coccidae (scale insects and mealy bugs)

The Homoptera all have piercing-sucking mouth parts and feed exclusively on plant sap Their method of feeding makes them especially effective as vectors of virus diseases Their long narrow beaks inject the inoculum deep into the tissues without wholesale destruction of cells Since the virus can multiply only in the presence of living cells, this is a decided advantage Insects that kill large numbers of cells around the feeding wounds would be less effective in bringing the virus in contact with living protoplasm Many insects of this order, which cause very little obvious direct injury to their host plants, are now considered pests of major economic importance because of their role in transmitting virus diseases A demand for more effective control of these species has followed the discovery of their role as vectors

The *aphids*, or plant lice, include a large number of vectors and transmit more different virus diseases than do the members of any other insect family More than twenty different species of aphids have been shown to be concerned in the transmission of a considerably larger number of different viruses Certain species such as *Myzus persicae* (Sulz) and *Macrosiphum gei* (Kalt) are known vectors for a dozen or more different viruses, while other species are more limited in this respect In general, there appears to be somewhat less specificity between the aphids and the viruses they transmit than there is between the leaf hoppers and the viruses spread by them Nevertheless there is abundant evidence of certain types of specificity among the

aphid vectors   On the other hand, there are numerous examples of a single species of aphis transmitting several different viruses, while such cases are rare among the leaf hoppers

The *leaf hoppers* rank next to the aphids in numerical importance as vectors of virus diseases   The following are a few examples of destructive virus diseases that are transmitted by the leaf hoppers indicated   curly top of sugar beet by *Eutettix tenellus* Baker, what appears to be the same or a similar disease in Argentina by *Agallia stictocollis* Stål, aster yellows by *Macrosteles divisa* (Uhl) and, to a lesser extent, by *Thamnotettix montanus* Van D and *T germinatus* Van D, streak of maize by *Cicadulina mbila* Naude, *C zeae*, and *C storeyi,* cranberry false blossom by *Euscelis striatulus* Fall, dwarf of rice by *Nephotettix apicalis* Motsch, and peach yellows by *Macropsis trimaculata* Fitch It will be noted that the vectors mentioned show a high degree of specificity for the diseases transmitted   In practically all cases, no other insect vectors are known for the particular virus transmitted although many have been tested   It is significant, also, that the vectors are rarely concerned in the transmission of any other virus although their host plants are often subject to several different virus diseases, and the host range of the virus transmitted is often very wide

The *plant hoppers*, or *lantern flies*, include several important vectors   *Peregrinus maidis* Ashm   was reported by Kunkel (1922) as a vector of corn mosaic in Hawaii   Ocfemia (1934) and Mungomery and Bell (1933) have shown that the Fiji disease of sugar cane is transmitted by the two fulgorids (*Perkinsiella vastatrix* Breddin and *P saccharicida* Kirk)

White flies have been shown to transmit a few virus diseases Leaf crinkle, or leaf curl, of cotton in Nigeria and Sudan is transmitted by *Bemisia gossypiperda* Misra and Lamba (Golding 1930, and Kirkpatrick 1930, 1931)   The disease is not transmitted by artificial inoculation, and the insect transmission appears to be biological and specific although Paoli (1931) claims that in Italian Somaliland it is transmitted by a leaf hopper (*Empoasca faciulis* Jac)   A similar disease of tobacco in Southern Rhodesia, probably caused by the same virus, is reported by Storey (1932b) as spread by *B gossypiperda*   The host range of the virus is not definitely known   Cassava mosaic is said to be transmitted in Africa by *B nigeriensis* Corb (Golding

1936) and by *B gossypiperda* var *mosaicivectura* (Lefevie 1935, Storey and Nichols 1938).

The *scale insects* and *mealy bugs* are common sucking insects and affect a wide variety of plants, but they have been shown to transmit relatively few virus diseases Elmer (1925) and Fajarado (1930) have claimed that mealy bugs are vectors of bean mosaic, and Ohtsky (1925) reports *Pseudococcus citri* as a vector of tomato and tobacco mosaic These reports, however, need further study and confirmation

4 *Hemiptera* —The insects of this order also have piercing-sucking mouth parts, and although many of them are plant feeders only relatively few are known to transmit virus diseases of plants A lace bug of the family Tingidae, *Piesma* (*Zosmenus*) *quadrata* Fieb , transmits the crinkle-leaf disease of sugar beet in Europe (Wille 1928, 1929) and "savoy," a similar although different disease of sugar beets in the United States, recently (Coons, Kotila, and Stewart 1937) has been shown to be spread by *P cinerea*

A few of the plant bugs have been incriminated in the transmission of certain virus diseases that are easily transmitted by mechanical means Most of them belong to the family Miridae For example, the tarnished plant bug (*Lygus pratensis* L) transmits the spindle tuber of potatoes (Goss 1928), potato mosaic (Elze 1927), and spinach blight (McClintock and Smith 1918) It is probable that such transmission is purely mechanical and incidental Smith (1934) has pointed out that this family of insects, although composing one of the largest groups of plant-feeding insects, is relatively insignificant as vectors of the viruses He believes that the toxicity of the insect's saliva for the plant tissues in the immediate vicinity of the feeding puncture is responsible for their inefficiency as vectors of virus diseases The zone of dead cells surrounding the feeding wound apparently keeps the virus from coming in contact with the protoplasm of the adjacent living cells The possibility of the saliva being toxic to the virus is also recognized, but there is little evidence available to support the theory

5 *Coleoptera* —Like the Orthoptera, the members of this order, the beetles and weevils, are all chewing insects and play a relatively small part in virus transmission About a half-dozen species have been incriminated, including the cucumber beetles

[*Diabrotica vittata* Fabr and *D duodecimpunctata* (Fabr)]
and the Colorado potato beetle (*Leptinotarsa decimlineata* Say),
which are reported to transmit the viruses of cucurbit mosaic
and spindle tuber of potatoes, respectively   Both these viruses
are transmitted readily by artificial sap inoculation, and the
beetles in all probability transmit the virus in a mechanical
manner

It will be seen from the foregoing that the sucking insects
as a group are much more effective as vectors of virus diseases
than the chewing insects   All sucking insects, however, are
not equally effective   Some that feed on virus-infested plants
appear to be unable to transmit the virus or else transmit it
mechanically and incidentally   Others transmit viruses so
effectively and with such regularity that it is evident that the
transmission is the result of a highly specialized adaptation

METHODS OF VIRUS TRANSMISSION BY INSECTS

If we consider the methods of virus transmission in the light
of the system of classification given in Chap IV, it will be seen
that they practically all fall in class 3, "Dissemination with
wounding "   Insect transmission of plant viruses without wound-
ing of the plant tissues is not known   There are examples of
purely mechanical transmission and examples of biological
transmission   There are examples of biological transmission
in which the insect is obligatory and also those in which the
insect is incidental

Mechanical transmission is the usual method of those vectors
with chewing mouth parts, such as the grasshoppers and beetles
Biological transmission is found only in the sucking insects, but
transmission by sucking insects is not always biological   It
has been shown that many sucking insects transmit viruses
mechanically and that certain aphids, such as *Myzus persicae*,
which transmit certain viruses biologically, may transmit others
in a purely mechanical manner   Kunkel (1935) listed 25 insects
that were believed to transmit viruses biologically   The list
has increased since then and includes approximately 35 species,
composed of about 20 leaf hoppers (including the fulgorids),
10 or more aphids, 2 or 3 white flies, and 3 or more species of
thrips   The nature of biological transmission of viruses by
insects is not clearly understood, and the term "biological

transmission" is used rather loosely   Biological transmission
of plant viruses by insects usually has one or more of the following
attributes

  1 An apparent multiplication or increase of the virus in the insect's body
  2 An incubation period in the body of the insect, that is, a necessary
period after feeding on infected plants before the insect becomes infective
or viruliferous
  3 A degree of specificity between the insect and the virus that it transmits
  4 An obligatory relationship
  5 A relation between the age or life stage of the insect and its ability to
transmit the virus
  6 Congenital transmission of the virus from one generation to the next

Each of these attributes must be considered in more detail
if we are to have a clear picture of what is known about the
biological relationship between insect and virus   The nature of
this relationship has occupied the attention of numerous investi-
gators during the past few years, and although there are many
conflicting viewpoints, much progress has been made   A critical
evaluation of some of the most important investigations in the
field has been published recently by Storey (1939)

MULTIPLICATION OF THE VIRUS IN THE INSECT BODY

The evidence for multiplication or increase of the virus in the
body of the insect vector is largely circumstantial and is based
chiefly on the fact that the virus is known to persist in the
insect's body for a relatively long time   Few quantitative
measurements have been made, and the evidence is somewhat
conflicting   It has been shown (Kunkel 1926) that the virus
of aster yellows may persist in the body of a viruliferous leaf-
hopper vector kept on nonsusceptible plants for the length of
its natural life, which may be as long as 100 days   In other
insects, where transmission is purely mechanical, the virus dis-
appears from the vector in a short time after feeding on an
infected plant, and the insect becomes noninfective   From this
it is concluded that the persistence of the virus for long periods
of time is to be explained by assuming a multiplication in the
insect's body   It seems reasonable to expect that the small
amount of the virus taken up in a short period of feeding on an
infected plant would be lost after feeding for such a long time
on nonsusceptible plants unless there were some multiplication

in the insect body   The chief objection to this assumption lies in the fact that the so-called "nonsusceptible" plants on which insects are fed are not completely immune and that a renewed supply of virus may be obtained from them   However, the virus is known to multiply in contact with living plant cells, and it seems reasonable that it could also multiply in the tissues of insect   The fact that it disappears so quickly from some insects and survives so long in others suggests the possibility of a multiplication of the virus in the latter

Further circumstantial evidence of multiplication of the virus of aster yellows in its vector is found in the fact, demonstrated by Kunkel (1937), that the virus may be inactivated in the insect's body by exposure to temperatures of 31 to 32 degrees for a sufficiently long time, but that if the exposure is of short duration, the insect only temporarily loses its ability to transmit the virus   The spontaneous regaining of the virus is interpreted by Kunkel as a multiplication of the small quantity of the virus not destroyed by the shorter heat treatment

Stronger evidence has been presented by Fukushi (1933, 1935, 1939), who has demonstrated that the virus of the dwarf disease of rice is congenitally transmitted through the eggs of its vector (*Nephotettix apicalis*)   He demonstrated transmission of the virus to the seventh generation   A single female vector infected 38 plants consecutively in 24-hour feeding periods, and the progeny of 15 eggs deposited by this female infected 201 plants without access to new sources of the virus   In one experiment, the progeny of one viruliferous egg, consisting of 26 leaf hoppers of five generations, inoculated more than 1,000 rice plants   Fukushi concludes that, since the amount of the virus originally contained in an egg or in the body of a nymph must be extremely minute, it seems necessary to postulate the multiplication of the infective principle within the insect

On the other hand, Freitag (1936) and Bennett and Wallace (1938) have presented evidence which leads them to conclude that the curly-top virus does not multiply in the body of *Eutettix tenellus*   These workers have shown by quantitative measurements that the virus content of viruliferous leaf hoppers decreases with the time elapsing after feeding on infected beets and that the time of survival in the vector decreased as the time of previous feeding on infected beets was decreased   Viruliferous

vectors that had become noninfective by long confinement on immune plants regained their infectivity when fed again on infected beets   There was no evidence of concentration of the virus in the salivary glands, and the evidence pointed to the blood, as the principal reservoir of the virus in the insect body

Evidence for the multiplication of animal viruses in their insect vectors is also somewhat contradictory   According to Davis, Frobisher, and Lloyd (1933), the virus of yellow fever does not increase in the body of *Aedes aegypti*   Quantitative measurements of the virus were made by diluting the crushed bodies of mosquitoes until no infection was obtained, when the diluted suspension was inoculated into susceptible animals In contrast to this, Merrill and TenBroeck (1934, 1935) showed that the virus of equine encephalomyelitis would multiply in the bodies of *A aegypti*   These workers artificially inoculated mosquitoes with the virus through 17 successive transfers, and in the last mosquito the concentration of the virus equalled that found in the first   These facts seem to justify the conclusion that this virus multiplies in the body of its insect vector   It appears that all viruses do not behave alike in regard to this phenomenon

Quantitative measurement of the virus in the bodies of insects is difficult and often may not be reliable when the technique involves the inoculation of plants with the juices of crushed insects   Black (1939) has shown that virus activity is often inhibited by insect juices   The juices of several species of aphid and leaf hopper effectively inhibited the infectivity of tobacco mosaic, and the juices of macerated clover leaf hoppers inhibited that of six other viruses   It was shown that the juices did not destroy the virus, because by suitable methods it could be separated in active form from the inhibiting juices   It was concluded that the inhibitory action was caused by action on the inoculated plant rather than on the virus itself

THE INCUBATION PERIOD IN THE INSECT BODY

It is a well-recognized fact that certain vectors of virus diseases do not become viruliferous until a certain time has elapsed after feeding upon an infected plant   This period of delay is usually called an "incubation" or a "latent" period although very little is known about the nature and cause of the delay.

The incubation period should not be confused with the so-called "threshold" period, which is the shortest length of time the vector must feed upon the infected plant in order to secure virus enough to become viruliferous   The threshold period has been determined for only a few species   Storey (1938) has determined it for *Cicadulina mbila* and the streak virus and found it to be approximately 5 minutes   For *Eutettix tenellus* and the curly-top virus it may be as short as 1 minute, according to Bennett and Wallace (1938)

The length of the incubation period varies with different insects and diseases from 20 minutes to 10 days or more and is modified by many influencing factors   The incubation period of the beet curly-top virus in the beet leaf hopper may be as short as 20 minutes when a large number of hoppers are used in the experiment   The shortest period obtained for a single leaf hopper is 7 hours (Severin 1921)   The minimum incubation period in the experiments of Bennett and Wallace (1938) was 4 hours   Swezy thinks that periods as short as 20 minutes or even 1 hour are not normal and can be explained by abnormal body structure which obstructs passage of the food and virus and causes its ejection or regurgitation shortly after it has been ingested   The possibility of an abnormal and unusually rapid passage of the virus through the body into the salivary glands is also recognized

The minimum incubation period for the virus of aster yellows in the adult leaf hopper, according to Kunkel (1926), is 10 days   A longer period is required in nymphs   Similar incubation periods have been shown for a number of other insect vectors, including *Cicadulina mbila* and the streak disease of maize (*Myzus persicae*), potato leaf roll (*Thrips tabaci*), and the yellow spot of pineapple   The length of the incubation period apparently is influenced by temperature, the higher the temperature, within limits, the shorter the period (Storey 1928)

Several theories have been offered to explain the necessity for an incubation period   It has been suggested by Smith (1934) that the virus particles may be absorbed on the surface of the tissues of the insect's mouth parts and that the insect becomes infective only after the absorbing surfaces have become saturated This, however, would not explain the incubation period when the

insect feeds on infected plants for a short period and is then transferred to nonsusceptible plants

The most probable explanation is based upon the theory that the virus particles must pass through the walls of the intestinal tract into the blood and from there into the salivary glands before they can be introduced into another plant   This hypothesis is supported by the fact that the insects in which an incubation period occurs (Homoptera and Hemiptera) are equipped with an esophageal valve that provides a one-way passage of the plant sap and prevents regurgitation

Swezy (1930) and Smith (1931a) have traced the course of dyes through leaf hoppers and aphids, respectively, and have shown that the dyes reach the salivary glands in a period of time shorter than the incubation period of the virus concerned   This does not invalidate the hypothesis, for the rate of diffusion of the virus particles may be much slower than the dyes used   Stanley (1937a) and others have shown recently that the protein molecule composing the virus of tobacco mosaic has a molecular weight greater than that of any other known protein, and filtration experiments have indicated that the particles of tobacco mosaic virus are among the smaller virus particles   Proteins of such high molecular weight would probably diffuse more slowly than dye particles

Storey (1928, 1932a, 1933) has thrown some light on the course of the virus in the insect by his studies on *C mbila* and the virus of maize streak   Storey discovered a strain of the vector that failed to become infective after feeding on infected plants   He showed that this failure was caused by the impermeability to the virus of the wall of the intestinal tract   When the intestinal wall was punctured with a fine needle after the insects had fed upon an infected plant, those insects which recovered were infective   Storey also was able to demonstrate the presence of the virus in the blood of normal insects after feeding on diseased plants as early as 5 to 6 hours before the insect became infective   It is highly probable that the normal course of the virus is from the digestive tract of the insect into the blood by diffusion, from the blood into the salivary glands, and from the salivary glands into the plant   An incubation period based on the time required for completing this course would more

nearly explain the known facts than any other hypothesis presented   This is about the only way an incubation period could be explained in those cases where the virus may be artificially transmitted by sap inoculation

Hamilton (1935) has attacked the problem in an interesting manner by feeding aphids (*M persicae*) on agar containing polonium, a radioactive substance, that could be traced by measurement with an electroscope   It was shown that the insect picks up the polonium and transmits it in constant amounts to leaves on which it subsequently feeds   It is concluded that the polonium, and in all probability the virus also, is transmitted through the insect's body and not mechanically on the stylets The same author (Watson 1936) has made a careful study of the factors affecting the transmission of a virus designated as Hy III by *M persicae* Sulz   The virus, which is readily transmitted by artificial sap inoculation, appears also to be transmitted biologically by the aphis   The amount of transmission obtained varied with changes of external conditions as well as with conditions within the insect   Of particular interest was the fact that when the insects were starved for a few hours before feeding a greater efficiency in transmission was obtained with feeding periods of 2 to 5 minutes on infected plants than with feeding periods of longer duration   This apparently was not true if the aphids were not previously starved   Two possible hypotheses were offered to explain these results   The first is based on the assumption that some of the virus is digested by the insect and that ' starvation may cause the glandular cells of the stomach wall to enter a resting phase, so that the digestive enzymes are not secreted until a short time after food has entered the mid-gut ''

The second hypothesis assumes the production of antibodies to the virus within the insect's body which, after a short time, confers partial immunity against the virus

The existence of a developmental cycle in the virus comparable to that found in certain parasitic protozoa transmitted by insects has been suggested by many workers, but there is no evidence whatever to support it   The conclusion of Stanley (1937*a*) that viruses are in reality proteins of high molecular weight, if confirmed, would seem to preclude the possibility of any such cyclic change

The latent period of the virus in the plant appears to vary with the number of insects used for inoculation, the shorter latent periods usually being obtained when a relatively large number of vectors are used   Severin (1931) and Carsner and Lackey (1929) have explained this by a theory of mass action which holds that, among other things, the length of the latent period varies in indirect proportion to the amount of inoculum introduced or to the number of vectors used in inoculation   This implies a cumulative effect of many small doses of virus injected by many different vectors   Storey (1938), on the other hand, feels that the evidence does not justify this conclusion, claiming that each separate inoculation is independent of all others and that several subinfective doses of a virus cannot unite in the plant to produce an infective dose

SPECIFICITY OF VIRUS TRANSMISSION BY INSECT VECTORS

There are numerous well-demonstrated cases of specificity between insect vectors and the viruses they transmit   The most striking examples are found in those virus diseases transmitted by leaf hoppers, including beet curly top and *Eutettix tenellus*, peach yellows and *Macropsis trimaculata*, cranberry false blossom and *Euscelis striatulus*, etc   As other examples of specific relationships may be mentioned leaf curl of cotton transmitted by *Bemisia gossypiperda* and pineapple yellow spot transmitted by *Thrips tabaci*   One should remember, however, that the evidence for specificity of transmission is generally of a negative character and that there is always the possibility of additional vectors being discovered

Although transmission is biological and there is a certain amount of specificity, the specificity is not always absolute, and transmission of a given disease is not always confined to one species of insect   Aster yellows, for many years thought to be transmitted only by *Macrosteles divisa*, is now known to be transmitted by three different species of leaf hopper (Severin 1934*b*)   Spotted wilt of tomato is transmitted by two species of thrips (Smith 1931*b*, Samuel and Bald 1931), rice dwarf by two species of leaf hopper, maize streak by three species of leaf hopper, and potato leaf roll is transmitted by at least six species of aphid   These viruses are all biologically transmitted, and each one is transmitted by closely related species of sucking insect

Group specificity in transmission is the most common condition among the aphid vectors

There are also insects that biologically transmit two distinct virus diseases, yet show a high degree of specificity for the two diseases and appear to be unable to transmit other viruses that affect their host plants   As examples may be mentioned *M divisa*, which transmits two distinct strains of aster yellows, *Myzus persicae*, which transmits biologically potato leaf roll and also dahlia mosaic (Brierly 1933), and *Aphis gossypii*, which is a vector of both "yellow flat" and mosaic of lilies

Specificity is manifested by certain insects that transmit selectively one virus from a plant affected with two or more distinct viruses   Hoggan (1929, 1930, 1931, 1933, 1934) has shown that, when *Myzus persicae*, *M solani*, and *Macrosiphum gei* are fed on tobacco plants affected with both cucumber mosaic and tobacco mosaic, they will transmit only the virus of cucumber mosaic This specificity may be based not on a biological relationship with the vectors but rather with the feeding habits of the insects on the tobacco plants, for they will readily transmit the tobacco virus from tomato plants   Smith (1931*a*) has reported selective transmission in which different viruses were consistently transmitted from the same compositely infected potato plant by insect and needle inoculations, respectively

In contrast to the high degree of specificity shown by certain insects and viruses, it is known that the yellow dwarf of onions may be transmitted readily by more than 50 species of aphids as well as a number of other sucking insects   Likewise, a single aphid (*M persicae* Sulz) is known to transmit more than 20 different viruses

The apparent specificity of certain groups of insects for viruses that produce similar symptoms has led to the use of insect relationships in the classification of viruses (Elze 1931*b*, Storey 1931, Johnson and Hoggan 1935, Smith 1934)   According to Smith there are four more or less distinct groups as follows (1) the mosaic group transmitted largely by aphids, (2) the yellows group transmitted by the leaf hoppers, (3) the group characterized by the production of spots with concentric rings, transmitted by thrips, and (4) those transmitted by the white flies and causing a thickening of the veins and abnormal leafy outgrowths on the lower side of the leaves   The extent to which insect relationships

TABLE I — THE CLASSIFICATION OF PLANT VIRUSES[1]

The plant viruses	Transmissible by sucking insects (A_1)	Not transmissible mechanically by plant extract (B_1)	Not transmissible by aphids (C_1)	Transmissible by leaf hoppers (D_1)
				Not transmissible by leaf hoppers (D)
			Transmissible by aphids (C)	Rosaceae susceptible (D_1)
				Rosaceae not susceptible (D_2)
		Transmissible mechanically by plant extract (B)	Longevity *in vitro* less than 7 days at 22°C (C_1)	Thermal death point below 60°C 10 min (D_1)
				Thermal death point 60°C or above 10 min (D)
			Longevity *in vitro* 7 days or more at 22°C (C)	Thermal death point below 80°C 10 min (D_1)
				Thermal death point 80°C, or above 10 min (D)
	Not transmissible by sucking insects (A_2)	Transmissible mechanically by plant extract (B_1)	Longevity *in vitro* 7 days or more at 22°C (C_1)	Thermal death point 60°C or above 10 min (D_1)
				Thermal death point less than 60°C 10 min (D)
			Longevity *in vitro* less than 7 days at 22°C (C)	Thermal death point 60°C or above, 10 min (D_1)
				Thermal death point less than 60°C 10 min (D)
		Not transmissible mechanically by plant extract (B)	Transmissible by grafting (C_1)	Potato susceptible (D_1)
				Potato not susceptible (D_2)
			Not transmissible by grafting so far as known (C_2)	Transmissible by other vegetative means (D_1)
				Not transmissible by other vegetative means (D_2)

[1] After Johnson and Hoggan (1935)

may be used in virus classification is shown in the scheme for classifying the major groups proposed by Johnson and Hoggan (1935) (see Table I)

The nature and cause of the specificity shown by certain insect vectors and the viruses they transmit have never been satisfactorily explained   A work of great significance in the study of this problem is that of Storey (1932a, 1933) in which it was shown that within a single species (*Cicadulina mbila* Naude) there are two strains or races, one of which is unable to transmit the virus of maize streak   These two races were designated as "inactive" and "active" according to their ability to transmit the virus By breeding experiments, the ability to transmit the virus was shown to be inherited as a dominant sex-linked character   Thus when active females were crossed with inactive males, the F_1 progeny were all active while the F_2 generation yielded active females and both active and inactive males   When active males were crossed with inactive females, the F_1 generation contained active females and inactive males   The F_2 of this cross produced both active and inactive females   No morphological differences between the races were observed   Further experiments showed that both active and inactive insects ingested the virus, which could be detected also in the feces of each race   In the inactive race, the virus was unable to diffuse through the intestinal wall into the blood and consequently did not reach the salivary glands When the intestinal walls of inactive insects were punctured with sharp needles after or just before feeding on infected plants, they became infective   The essential difference between the races appears to lie in the unequal permeability to the virus of the intestinal walls   This is a very significant discovery and suggests that specific selective permeability of the intestinal walls of the insect vectors may account for much of the specificity observed

Individual differences in ability to transmit a virus have not been so well demonstrated for any other vector of plant viruses, but Huff (1931) has reported a similar condition in two species of mosquito (*Culex spp*) in relation to *Plasmodium cathemerium*, the cause of bird malaria   The ability of these vectors to transmit the pathogen is inherited, according to Huff, as a simple Mendelian recessive factor

Bennett and Wallace (1938) have shown that several species of insects which are not vectors of curly top of beet, including *M*

persicae, A *rumicis, Aceratogallis californiaca, Hercothrips femoralis,* and others, acquired the virus by feeding on infected beets and retained it for periods ranging from 1 to 21 days but were unable to transmit it to sugar beets It was concluded that the inability of these insects to transmit the virus was caused by the presence of an effective barrier to virus passage in some part of the insect's body

THE OBLIGATORY NATURE OF INSECT TRANSMISSION OF CERTAIN VIRUSES

When a virus can be transmitted only by one or two closely related insects and cannot be transmitted artificially (except by grafting), the insect transmission is considered obligatory There are few, if any, viruses that cannot be transmitted by grafting Failure to transmit a disease by grafting would be strong presumptive evidence that it is not caused by a virus Obligatory insect transmission obviously must be based on negative evidence, and there is always the possibility that a suitable technique for artificial transmission will be discovered Nevertheless, failure of all recognized methods of transmitting the virus except by grafting and through the agency of specific insect vectors, is considered good evidence that transmission is not mechanical but that a biological relationship is concerned The following virus diseases are good examples of those which have not been transmitted artificially except by grafting, and the insect vectors indicated are considered essential for the spread of the disease in nature The list, of course, is subject to modification by new evidence

1 Aster yellows [*Macrosteles divisa* (Uhl), *Thamnotettix montanus* Van D , and *T germinatus* Van D]

2 Dwarf of rice (*Nephotettix apicalis* Motsch and *Deltocephalis dorsalis* Motsch)

3 Peach yellows (*Macropsis trimaculata* Fitch)

4 Cranberry false blossom (*Euscelis striatulus* Fall)

5 Streak of corn [*Cicadulina mbila* (China), *C storeyi* China and *C zeae* China]

6 Fiji disease of sugar cane (*Perkinsiella vastatrix* Breddin and *P saccharicida* Kirk)

7 Cotton leaf curl (*Bemisia gossypiperda* Misra and Lamba)

8 Leaf curl of sugar beet (*Piesma quadrata* Fieb)

Johnson and Hoggan (1935) list 28 viruses that are transmitted specifically by sucking insects and are not transmissible mechan-

ically by plant extracts, and there have been several additions since the tabulation was made

THE RELATION OF THE AGE OR LIFE STAGE OF THE INSECT VECTOR AND ITS ABILITY TO TRANSMIT THE VIRUS

Another indication of biological transmission of viruses is offered by certain vectors that are unable to transmit the virus in the nymphal or larval stages   Kunkel (1926) showed that nymphs of *Macrosteles divisa* (Uhl) often were unable to transmit the virus of aster yellows   This was explained by pointing out that the minimum incubation period of the insect was longer than the period of metamorphosis

A somewhat different relationship exists between the thrips (*Thrips tabaci* and *Frankliniella lycopersici*) and the viruses they transmit   Bald and Samuel (1931) have shown that, in order to transmit the virus of the spotted wilt of tomato, *F lycopersici* must have fed in the larval stage on infected plants   The adults appear unable to pick up the virus by feeding   Linford (1932) showed the same relationship for *T tabaci* and the yellow spot of pineapple   Smith (1932) confirmed this peculiar relationship in transmitting the spotted wilt of tomato with *T tabaci*

The relationship here is more difficult to explain than that between *M divisa* and the aster-yellows virus because the thrips live in the larval stage much longer than the incubation period, which is rarely longer than 10 days   It is still more difficult to explain when we recall that the virus of spotted wilt may be transmitted mechanically by sap inoculation   The explanation in all probability must be sought in the anatomy or physiology of the digestive system of the insects

CONGENITAL TRANSMISSION OF VIRUS IN THE INSECT VECTOR

Despite the intricate biological relationships between viruses and their insect vectors, congenital transmission of viruses appears to be the exception rather than the rule   As early as 1918, McClintock and Smith reported that the virus of spinach blight was transmitted from infective aphids (*Myzus persicae* and *Macrosiphum gei*) to their viviparously produced young through four generations   These conclusions were based on the assumption that the host on which the young were reared was

immune to the virus, an assumption later proved to be erroneous Hoggan (1933) and others have been able to show that such congenital transmission does not occur in these aphids Similar proof of the noninheritance of the virus of potato leaf roll by aphids has been obtained by Elze (1927) and Smith (1929)

Many leaf-hopper vectors do not transmit the virus to their offspring Bennett and Wallace (1938) have shown that the virus of curly top is not transmitted through the eggs Similar conclusions were reached by Kunkel (1926) in regard to the aster-yellows virus and *Macrosteles divisa* and by Storey (1928) for maize streak and *Cicadulina mbila*

However, in 1933 and 1939 Fukushi presented evidence to show that the virus of the dwarf disease (stunt) of rice is congenitally transmitted through the eggs of the vector (*Nephotettix apicalis* Motsch var *cincticeps* Uhl) Insects of known history, males and females in pairs, some infective and some noninfective, were placed on healthy rice plants enclosed in glass tubes where they were allowed to remain only 1 day, being transferred to new healthy plants each day Eggs were deposited in the lower part of the leaf sheath As the young nymphs emerged from the eggs, they were transferred individually to healthy plants before they had an opportunity to feed on the plants in which the eggs were deposited They were kept on these plants for 2 months or longer

The results indicated that the virus was transmitted through the eggs to the nymphs When infective females were paired with infective males, the majority of the offspring in all progenies was infective When infective females were paired with noninfective males, both infective and noninfective progenies were found, but when noninfective females were paired with infective males, none of the progenies was infective

Fukushi states that when eggs were deposited in infected plants by noninfective females none of the progeny was infective This is added evidence that the eggs become infected in the early stages of development in the ovary Since some individuals of the progenies from infective females were noninfective, it was concluded that some of the ovaries may escape infection Because of the significance and striking nature of these results the tabulated summary of Fukushi's experiments is given in Table II

THE EFFECT OF THE VIRUS ON THE INSECT VECTOR

In view of the close biological relationship shown by certain viruses and their insect vectors, one naturally is interested in knowing what effect the virus has upon the insect   Is the insect infected with a virus disease like the plant?   This is perhaps only

TABLE II —CONGENITAL TRANSMISSION OF VIRUS OF RICE DWARF IN THE LEAF HOPPER (*Nephotettix apicalis*)*

Parents		No of progeny tested	No of viruliferous progeny
Female	Male		
Infective female × infective male			
e279–4–3(♀)	e279–4–4(♂)	7	5
e'34(♀)	e'29(♂)	14	13
e'39(♀)	e'36(♂)	8	8
e'49(♀)	e'68(♂)	4	4
e'53(♀)	e'58(♂)	1	1
Infective female × noninfective male			
e279(♀)	a(♂)	13	13
e151–4(♀)	b(♂)	16	15
e151–1(♀)	c(♂)	26	17
e151–4–4(♀)	d(♂)	6	0
e279–4(♀)	e(♂)	35	33
e279–1(♀)	f(♂)	27	0
e151–1–16(♀)	g(♂)	30	0
e'51(♀)	h(♂)	8	8
e279–4–5–3–3(♀)	i(♂)	5	5
e'62(♀)	j(♂)	2	2
e'69(♀)	k(♂)	2	0
e'65(♀)	l(♂)	1	1
e'61(♀)	m(♂)	12	6
Noninfective female × infective male			
a(♀)	e151–1–22(♂)	9	0
b(♀)	e151–1–13(♂)	19	0
c(♀)	e'151–1–13(♂)	5	0
d(♀)	e'47(♂)	9	0
e(♀)	e279–4–32(♂)	14	0
f(♀)	e'64(♂)	4	0
g(♀)	e'72(♂)	3	0

* After Fukushi   ♂ and ♀ denote infective male and female, respectively, and ♂ and ♀ stand for noninfective male and female

an academic question and may depend entirely upon our definition of a disease   No one has ever observed a detrimental effect

of plant viruses upon the insect vectors There are several very destructive virus diseases of insects, and it is obvious that the effect of the plant viruses on the insects is in no way comparable to these Dobroscky (1931) was unable to find by histological methods any lesion or any visible effect of the virus of aster yellows on the leaf-hopper vector Smith (1934) stated that he, too, was unable to find any visible effect of two potato viruses on aphids Blattny (1931), on the other hand, found that the areola around the nucleus of the cells of the salivary glands was darker in infective aphids than in noninfective ones Hartzell (1937) reports the presence of intracellular inclusions in the cells of the intestinal wall and salivary glands of viruliferous specimens of *Macropsis trimaculata*, the vector of peach yellows These bodies were similar to those observed in the cells of infected peach tissue, and they were not found in healthy peach tissue or in nonviruliferous leaf hoppers Similar bodies were observed in viruliferous specimens of *Macrosteles divisa* and in asters affected with yellows The observations were made on living tissues and unstained fixed material This is the first report of inclusion bodies in the insect vectors of plant viruses It shows that the virus is in intimate contact with the protoplasm of the cells of the insects but does not necessarily mean that the insects are affected with a virus disease Whatever may be the significance of the cell inclusions, it is probably true that the viruses are less injurious to the insect vectors than to plants

It has been observed that the sucking insects which include the specific vectors, are all provided with a mycetome It often has been suggested that the mycetome or its symbiotic microorganism may be in some way related to the viruses transmitted by the insect However, no convincing evidence of such a relationship has been presented Carter (1939) failed to find any correlation between the presence of symbiotes in *Cicadulina mbila* and their ability to transmit the virus of maize streak

Stanley (1937a) has shown that one of the chief effects of the tobacco-mosaic virus on the tobacco plant is to dominate protein metabolism so that abnormally large amounts of a foreign protein (the virus) are synthesized Since there is some evidence that the virus multiplies in the insect vectors, it is likely that the virus modifies the nitrogen metabolism of the insect It is difficult to determine to what extent this effect is injurious It

is entirely possible that the virus in some way may be beneficial to the insect vector   Stanley (1937*b*) and Bawden and Pirie (1937) have concluded that the soluble-protein content of tobacco plants affected with tobacco mosaic is considerably higher than that of healthy plants   Although this conclusion has been questioned by Martin, Balls, and McKinney (1938) and the total protein is not increased by all viruses in all plants, it is agreed that the nitrogen metabolism of the diseased plant is greatly altered   It is not known in what form the modified protein occurs, but apparently much of it is the actual virus protein   It is well known that the protein supply is the limiting factor in the nutrition of insects which feed on the sap of plants and that they must ingest very large quantities of water and carbohydrates in order to get enough nitrogenous food for normal nutrition   Mumford and Hey (1930) have pointed out that a high nitrogen content of plants stimulates reproduction in insects which feed upon them and in general makes the plant more susceptible to insect attacks   A higher protein content or a higher percentage of a more suitable protein in available form would be of decided benefit to the sucking insects   It is not yet known whether insects are able to utilize the virus proteins as food or whether the virus proteins in any way influence their metabolism   Watson (1936), in an effort to explain certain facts concerning the transmission of a virus by *Myzus persicae*, has suggested that some of the virus may be digested by the insects and that only a part of the ingested virus is needed for effective transmission   Feeding experiments with the various vectors and purified virus proteins should throw light on some of the obscure relationships between insect and vector

   Complicated structures or complicated adaptations rarely occur in nature without serving some important function   They usually arise through natural selection on the basis of their survival values   One is therefore inclined to look for the possible benefits derived from the association by each of the associated entities   Numerous cases have been cited of the evolution of an association of insects and microorganisms for mutual benefit   There is no convincing reason why association of insects and viruses may not have arisen in a similar manner   It requires very little imagination to see such a beneficial association between the leaf hopper (*Eutettix tenellus*) and the curly-top virus   According

to Carter (1930), this insect is very susceptible to high humidity and thrives best in arid regions in relatively thin stands of its host plants   It will not thrive in heavy luxuriant stands of weeds or sugar beets   If sugar beets are well developed in a good stand when the leaf hoppers migrate to the beet fields, the hoppers do not multiply rapidly on account of the high relative humidity and do not build up large populations   On the other hand, if the hoppers migrate to the field when the plants are small, the unfavorable humidity of dense stands is precluded by infecting the plants with the curly-top virus and preventing their normal development   If the leaf hoppers were not vectors of the curly-top virus, the sugar beets would grow normally and in all probability would not be a favored host of the leaf hopper

The question of whether a virus-infected plant is a more favorable host than a healthy plant for the insect vector has been given very little attention in virus studies   It is of interest, therefore, that Carter (1939a) in a recent study of populations of *Thrips tabaci*, with reference to transmission of pineapple yellow spot, has found that the populations on diseased weeds (*Emilia sonchifolia*) are consistently higher than those on healthy plants   It is concluded that infected plants are more suitable hosts for the vector because, as a result of delayed maturity, they persist for a longer time than healthy plants, and because the excessively curled leaves afford valuable shelter for the vector

The benefits, if any, derived by the vectors of other virus diseases are not so evident   The dependence of the virus upon the insects for transmission is obvious and leaves no doubt of the benefits derived from the association by the virus   Whatever the significance of the association may be, there is yet much to learn about the relationships between the viruses and their vectors   The problem offers a fascinating field of research, and its solution should be of fundamental significance in the fields of both plant and animal pathology

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CHAPTER IX

INSECTS AND VIRUS DISEASES (*Continued*)

SELECTED EXAMPLES OF VIRUS DISEASES TRANSMITTED BY INSECTS

The number of virus diseases of plants known to be transmitted by insects is so very large that it is impractical to discuss them all in detail. Smith (1937*a*) lists a total of 136 viruses, excluding the numerous strains of those given numerical rank, and nearly all of them are transmitted by one or more species of insects. Holmes (1939) has applied Latin binomials to 89 species and 30 varieties. Although there is wide variation in the relationships between the viruses and their insect vectors, the principles involved in transmission are essentially the same for many of the virus diseases. Moreover, the information about the methods of insect transmission is meager for some of them. Therefore, only a few of the better known virus diseases, selected to illustrate representative types of transmission, will be discussed, and these will be treated primarily from the standpoint of transmission phenomena.

An effort has been made to arrange the diseases in groups according to the methods by which they are transmitted in nature, with particular reference to insect vectors. For a number of obvious reasons, it is not possible to draw sharp lines between the different groups. It is believed, however, that the arrangement followed will aid in visualizing the important features of insect transmission of the virus diseases.

1. TRANSMISSION BY MECHANICAL SAP INOCULATION; INSECT TRANSMISSION PURELY MECHANICAL

Potato Spindle Tuber (Solanum Virus 12*).—The name "spindle tuber" was applied to this disease by Martin in 1922. Its infectious nature was established first by Schultz and Folsom (1923) who showed that it could be transmitted by aphids and

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* Classification of Kenneth Smith (1937*a*)

also by artificial sap inoculation   It is selected as an example of a highly infectious virus transmitted mechanically and non-specifically by many different insects   Spindle tuber has been found to be distributed generally throughout the potato-growing regions of the United States, according to Smith (1934), it is not known in Europe   Because of the rapidity with which the disease spreads in nature and the difficulty of detecting infected plants in early stages of development, spindle tuber is one of the most difficult to control of all the virus diseases affecting potatoes
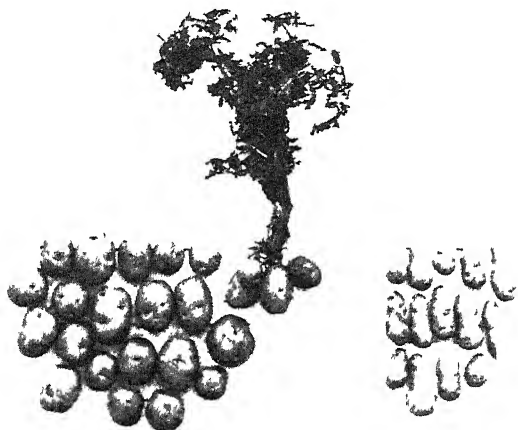
Fig 135 —Potato spindle tuber   The tubers on the left are healthy, those on the right are affected with spindle tuber

The most characteristic symptom of this disease, as indicated by the name, is the tendency of tubers to become excessively elongate, forming a spindle-shaped tuber tapering most at the bud end (Fig 135)   The color of the tubers of red varieties become less intense, the eyes at the apex are shallow and more numerous, with protruding "eyebrows "   The yield of market-able tubers is always greatly reduced

The symptoms of spindle tuber have been confused with those of unmottled curly dwarf, a disease very similar in many respects but thought by some workers to be caused by a distinct virus The most extensive comparative study of the two diseases has been made by Goss (1930)   Both diseases apparently have a narrow host range, as interspecific inoculations have failed to transmit them to other solanaceous species

Transmission of Spindle Tuber —Spindle tuber is highly infectious and is readily transmitted by many different agencies It is easily transmitted by various methods of artificial sap inoculation   Goss (1931) has shown that spindle tuber, as well as unmottled curly dwarf, is transmitted readily by contact of cut seed pieces and by the cutting knife, as many as four successive seed pieces being successfully inoculated with the knife following its use in cutting a diseased tuber

As would be expected with such a highly infectious disease, it is transmitted readily by many different insects   Goss (1931) tested the insects that were most prevalent on potatoes   in Nebraska and succeeded in demonstrating transmission by the following grasshoppers (*Melanoplus spp*), flea beetles (*Epitrix cucumerus* Harris and *Systena taeniata* Say), the leaf beetle [*Disonycha triangularis* (Day)], the tarnished plant bug (*Lygus pratensis* L), and the larvae of the Colorado potato beetle (*Leptinotarsa decimlineata* Say)   A small number of trials with the leaf hopper (*Euscelis eritiosus*) gave negative results   Transmission by aphids (*Macrosiphum gei* and *Myzus persicae*) had previously been demonstrated by Schultz and Folsom (1923) Unmottled curly dwarf was transmitted by the same species of insects with the exception of the leaf beetle (*D triangularis*)

The results of these experiments indicate strongly that insect transmission is entirely mechanical and that almost any insect that feeds on the potato and moves from plant to plant is a potential vector of the virus   In all probability, this fact accounts for the very rapid spread of spindle tuber under field conditions Brentzel (1935) has reported an experiment showing the rapidity of spread of spindle tuber in North Dakota   Beginning with selected healthy seed stock, 1,000 tubers, selected at random, were replanted for 3 successive years   No precautions were taken to prevent the spread of the disease   After 3 years, 95 per cent of the plants were definitely affected with the disease   Goss (1929) reported a spread of 42 4 per cent by spindle tuber in Nebraska after 4 years, as compared with 9 7 per cent spread by leaf roll   Mild mosaic and rugose mosaic spread more slowly than leaf roll   In one year, when insects were more abundant, there was an increase in spindle tuber infection from 14 to 42 per cent

Control of spindle tuber is relatively difficult and obviously depends upon rigid inspection of seed stock, early recognition of

affected plants, prompt roguing, careful bin selection of seed tubers, and as effective control as possible of all insects

Tobacco Mosaic (Nicotiana Virus 1) —There are several different viruses that attack tobacco   One of these (Nicotiana virus 1) has been studied more intensively than any other plant virus   This is presumably the virus or one of the viruses concerned in the classical work of Allard (1914 to 1917) and that of other pioneers in virus investigations   It is the first virus to

Fig 136 —Tobacco leaves showing the symptoms caused by two strains of common tobacco mosaic   (*After Valleau and Johnson*)

be isolated in the form of a pure crystalline protein (Stanley 1937*a*)   It causes a variable mosaic pattern of light- and dark-green areas on tobacco leaves (Fig 136) but causes many different symptoms on other plants

Transmission of Tobacco Mosaic —Even though this virus disease has been studied intensively, there is still much confusion in regard to the methods of transmission   For many years, it was thought to be transmitted largely by aphids   Although it was on the tobacco plant that a virus disease was first proved to

be transmitted by aphids (Allard 1917), these insects apparently are not important vectors of this particular virus   The tobacco plant is not a favorable host for aphids, and Hoggan (1930, 1931, 1934) has shown that *Myzus persicae*, *M   pseudosolani*, *M cucumflexus*, and *Macrosiphum solanifolii*, the most common aphids on tobacco, do not transmit this virus from tobacco to tobacco, although they will transmit it from tomato to tobacco and other solanaceous hosts   However, these insects will transmit the cucumber mosaic from tobacco to tobacco and from tobacco to other hosts   This virus (Nicotiana virus 1) is highly infectious by artificial sap inoculation, and it is probable that under field conditions it is transmitted chiefly by man in the various operations of cultivation

Little is known of the nature of insect transmission of this virus   It is difficult to understand why the aphids do not transmit mechanically such a highly infectious virus   Also, the differential and specific transmission by the aphids of the various viruses that affect tobacco suggest some sort of biological relationship   There is still much to learn about the subject   The isolation of this virus in pure crystalline form (Stanley 1937*a*, 1938*a*, 1938*b*) should make it possible to learn a great deal more about the property of the virus and about the ways in which it may be transmitted

Yellow Dwarf of Onions (Allium Virus 1) —Yellow dwarf is a relatively new disease of onions, having been observed for the first time in Iowa in 1927   It was very destructive in local areas and spread rapidly until methods of control were devised   The virus nature of the disease was established in 1929 by Melhus, Reddy, Henderson, and Vestal   More detailed investigations have been reported by Drake, Harris, and Tate (1932, 1933) and Henderson (1935)

The most characteristic symptoms of yellow dwarf are the yellowing, crinkling, and dwarfing of the leaves and flower stalks (Fig 137)   Underdeveloped bulbs of little commercial value are produced by diseased plants   Infected plants produce normal seed but about 30 per cent less than healthy plants

Transmission of Yellow Dwarf —Yellow dwarf is readily transmitted by artificial sap inoculation and by more than 50 different species of aphids   Of these the following species are most commonly found on onions and are probably of greatest impor-

tance *Macrosiphum pisi* (Kalt), *Aphis rumicis* L , *Aphis heli-anthi* Monell, *Hyalopterus atriplicus* L , and *Rhopalosiphum prunifoliae* Fitch   Transmission of these insects apparently is entirely mechanical   If there is an incubation period in the insect, it is extremely short   Even though the disease is trans-mitted readily by artificial sap inoculation, certain insects such as grasshoppers, beetles, cutworms, coleopterous larvae, onion maggots thrips, and bulb mites do not transmit the disease

Fig 137 —Yellow dwarf of onion   Four diseased plants compared with the two healthy plants in the center   (*After Henderson*)

(Drake *et al* 1933)   The onion is not a preferred host for any of the aphid vectors, and none of them breeds on the onion   In addition to the aphids, the six-spotted leaf hopper (*Macrosteles divisa*) and a mealy bug (*Phenacoccus sp*) have been reported as vectors

The latent period of the disease in onions is about ten days The virus is inactivated in 112 hours by aging *in vitro* and in dried onion leaves   The virus is not transmitted in the seed of the onion   It survives the winter chiefly in infected bulbs, either

volunteer plants or in commercial sets   The virus does not over-winter in the soil and is not spread to any extent by cultivation practices

Rather effective control has been secured by a system of greenhouse indexing of onion sets and by using sets that have been grown in regions where yellow dwarf does not occur   Good results have been obtained also by spraying to control the aphids The destruction of volunteer onions is likewise of some value By the combined use of these practices, all based on a knowledge of the various means of transmission, the prevalence of the disease in a given area was reduced from 40 per cent in 1928 to a trace in 1934

Cucumber Mosaic (Cucumis Virus 1) —Cucumbers are affected by more than one virus, but the one designated by Johnson (1927) as cucumber mosaic virus 1 is the most prevalent and is the cause of the disease described in detail by Doolittle (1920) The disease is very destructive and is a limiting factor in cucumber culture in many regions where the crop has been grown intensively over a period of years   It is destructive to greenhouse plants as well as to those grown in the field

The virus is not confined to cucumbers but has a relatively wide host range, affecting not only other cucurbits but also many distantly related species   Furthermore many common weeds may act as carriers of the virus   It commonly survives the winter in the roots of perennial weeds, and these may serve as sources of infection for the cultivated crop   The frequency of weed infection makes practical control in the field very difficult

The symptoms appear first on the young leaves as a typical mosaic pattern of light and darker green areas (Fig 138)   The leaves are slightly curled, and, as they grow older, then color becomes lighter yellow   Eventually they die, becoming dry, brown, and brittle   Diseased plants are greatly stunted, and the yield is strikingly decreased   Affected fruits are mottled with light- and dark-green areas which are raised above the surface to form characteristic warty protuberances   The cucumbers are distorted and undersized, the quality of the flesh is poor, and the market value is almost negligible

Transmission of Cucumber Mosaic —Primary infection usually arises from a virus that has survived the winter in the roots of susceptible weeds, such as milkweed (*Asclepias syriaca*), poke-

weed (*Phytalacca decandra*), and the wild ground cherry (*Physalis sp*)   The virus may be transmitted also in the seeds of the wild cucumber (*Micrompelis lobata*) and in a very small percentage of the seeds of muskmelons (Kendrick 1934)

Cucumber mosaic is readily transmitted by artificial sap inoculation, being commonly spread in pruning, picking, and cultivating operations   It is also transmitted by insects, chiefly *Aphis gossypii* Glov , although it may be transmitted less readily by *Myzus persicae* Sulz , *M pseudosolani* Theob , *M cucumflexus* Buckt , and *Macrosiphum gei* Koch (Hoggan 1930)   It is believed by some workers (Doolittle and Walker 1928) that
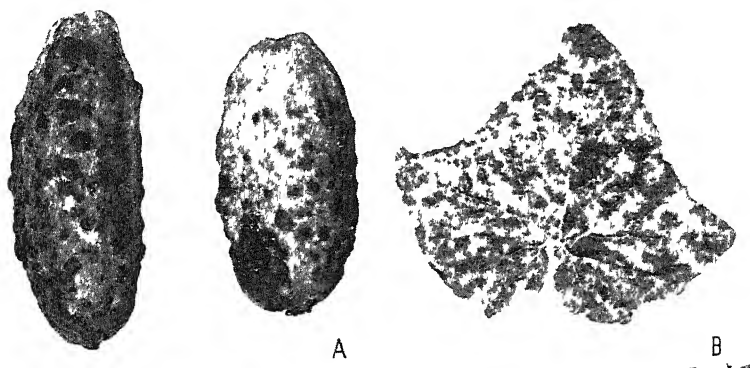
FIG 138 —Cucumber mosaic   *A* on fruits *B*, on a leaf   (*After Doolittle*)

aphid transmission of this virus is purely mechanical since the aphids lose their infectivity after a very short period of feeding However, the question is open for further study because of the selective transmission of the cucumber virus by certain species of aphids from tobacco plants affected with both cucumber-mosaic virus and tobacco-mosaic virus, as demonstrated by Hoggan (1929, 1930, 1931, 1933)

In addition to aphids, the striped cucumber beetles (*Diabrotica vittata* Fabr and *D duodecimpunctata* Oliv) may transmit the virus to a considerable extent   Transmission of the virus by these chewing insects apparently is purely mechanical

Cucumber mosaic may be controlled readily in greenhouses by thorough insect control and by careful roguing of infected plants as soon as the symptoms appear (Doolittle 1924)   In the field, effective control is not so practical   A reasonable degree of

control has been reported in local areas by thorough eradication of the weed carriers in and about the fields (Doolittle and Walker 1926) However, this has not been practical for the individual grower

Western Celery Mosaic (Apium Virus 1) —There are several viruses that affect celery some of which are better known for their occurrence on other economic crops   The western celery mosaic, however, is primarily a disease of celery, and its host range appears to be limited to the Umbelliferae   It is a disease of major importance to the celery industry of California   The disease has been described and studied extensively by Severin and Freitag (1938)

The symptoms of western celery mosaic are yellow, mottled foliage, twisted, cupped, and malformed leaflets, and a general stunting of the plant   A shortening of the petioles of the central leaflet and a horizontal position of the petioles of the outer leaflets gives the top of the plant a flattened appearance   Necrotic spots and streaks may develop on leaves and petioles in later stages of infection

Transmission of Western Celery Mosaic —The disease is readily transmitted by artificial sap inoculation, the latent period varying from 10 to 16 days   It has been demonstrated that the virus may be successfully transmitted by any of 11 different species of aphids that breed on celery in California   Transmission appears to be entirely mechanical, and there is no specific aphid vector   The virus is retained by the aphids for relatively short periods, varying from 1 to 10 hours   The aphids found on celery in California have been adequately described by Essig (1938)

There are numerous other viruses that fall within this group, most of which are transmitted in nature by several species of aphid   Owing to a lack of sufficient data on insect transmission of these viruses, it is often difficult to determine whether some of them should be placed in this or the following group

2 TRANSMISSION BY APHIDS, SHOWING GROUP SPECIFICITY, INSECT TRANSMISSION NOT ENTIRELY MECHANICAL

Sugar-cane Mosaic (Saccharum Virus 1) —Mosaic is one of the major diseases of sugar cane wherever the crop is grown Early symptoms consist of irregular chlorotic streaks on the

leaves, but later symptoms vary considerably (Fig 139)   The chlorosis becomes more marked, the plants are badly stunted, and necrotic lesions are often formed on the canes   The yields are greatly reduced   Sugar-cane mosaic affects corn, sorghum, millet, and several species of wild grass   In Louisiana, sorghum (*Holcus sorghum*), pearl millet (*Pennisetum glaucum*), crab grass (*Syntherisma sanguinalis*), bull grass (*Paspalum bascianum*), giant foxtail (*Chaetochloa magna*), and *Brachiaria platyphylla* are frequently found naturally infected in the vicinity of sugar-cane fields (Brandes and Klaphaak 1923)
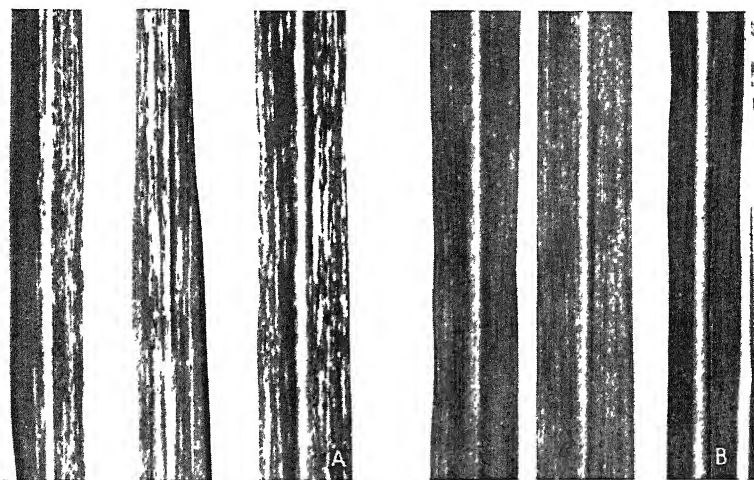
Fig 139 —Sugar cane leaves affected with a severe strain (*A*) and a mild strain (*B*) of mosaic   (*Photographs by courtesy of I L Forbes*)

Transmission of Sugar-cane Mosaic—The disease is transmitted by vegetative propagation, by artificial sap inoculation and by insects, the most important of which is the so-called ' corn aphid" (*Aphis maidis* Fitch) (Figs 140 and 141)   When it was first reported by Brandes (1920) that the virus was transmitted by this insect, the practical importance of the vector was questioned by several writers (Wolcott 1921), because sugar cane is not a preferred host of *A maidis*   The insect cannot be reared continuously on sugar cane and feeds on the plant only when other preferred grasses are not available   Later work, however, has established the fact that this insect is an effective vector

In nature, the aphids breed abundantly upon the wild grasses that are known to carry the virus When these grasses are repeatedly cut down in the process of cultivation, the aphids migrate to the sugar cane and inoculate it with the virus (Brandes and Klaphaak 1923) Practical field experience has verified this sequence of events as reported in 1928 by Wolcott, who discusses the facts as they influence the control of the disease Because cultivation of the cane cannot be dispensed with entirely, inoculation by aphids migrating from the cut grasses cannot be avoided
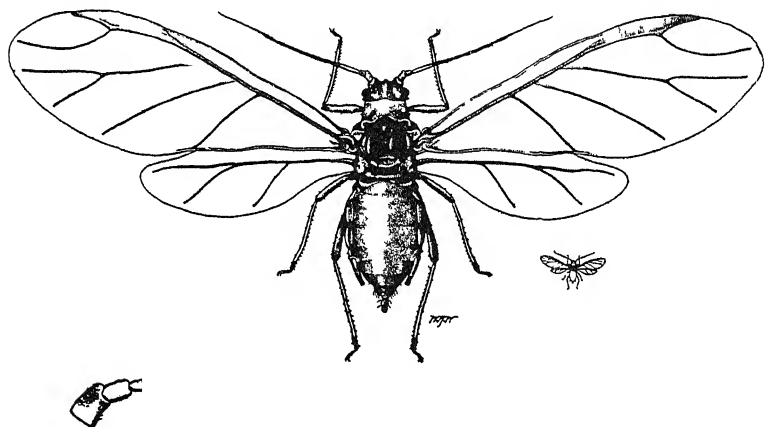
Fig 140 —*Aphis maidis* (an adult alate male), the principal vector of sugar cane mosaic A drawing to show its distinctive markings (*Courtesy of J W Ingram*)

The most successful control has been obtained through the use of mosaic-resistant selections of sugar cane

A notable contribution to the mechanics of inoculation of plant viruses by sucking insects was made in the study of sugar-cane mosaic by Brandes (1923) who studied the histological relationships between the mouthparts of *A maidis* and the tissues of the sugar-cane plant He showed that the aphids invariably seek out the phloem and that a copious flow of saliva into the living tissues takes place during penetration and feeding His conclusion that mosaic infection occurs in this way has been amply confirmed by later investigations with many viruses and vectors

A second vector was reported by Ingram and Summers in 1936 These authors were successful in transmitting the virus

by the rusty plum aphid [*Hysteroneura setariae* (Thomas)]   This insect was not so effective as *A   maidis*, transmitting the virus only 5 2 per cent of the trials compared with 23 3 per cent transmission by *A   maidis*   The rusty plum aphid, however, was much more abundant than the corn aphid on sugar cane, this plant being one of its preferred hosts throughout the year   The corn aphis is found on sugar cane only in late winter and early spring when other hosts are scarce   The rusty plum aphid breeds also on a number of wild grasses which are common hosts of sugar-cane mosaic   For these reasons, Ingram and Summers considered it to be a vector of much significance in the spread of sugar-cane mosaic
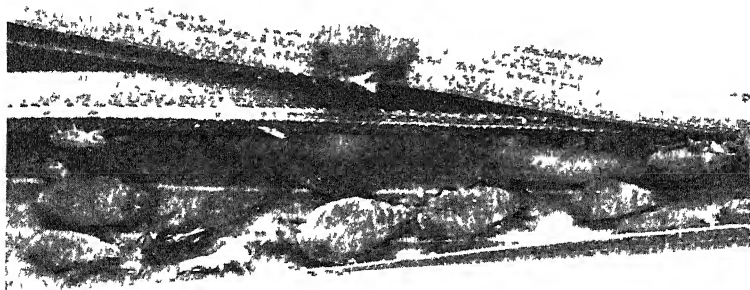
Fig 141 —A colony of *Aphis maidis* feeding on a grass leaf   (*Photograph by courtesy of J W Ingram*)

Ingram and Summers (1938) report the transmission of the virus in two instances with the aphid *Toxoptera graminum* Rond , which also was found on sugar cane   The number of trials was too small in this case to justify the conclusion that this insect is a vector of much significance   More recently, Tate and Vandenberg (1939), working in Puerto Rico, have incriminated another vector, namely, *Carolinaia cyperi* Ainslie, an aphid that is found abundantly in and near sugar-cane fields on its native host *Cyperus rotundus*   Since the virus is readily transmitted by artificial sap inoculation, it is probable that several other insects may be found that are capable of transmitting the disease to a limited extent

Sugar-cane mosaic is not caused by a single virus, several strains of distinctly different virulence and causing different

symptoms have been recognized   In Louisiana, a green and a yellow strain are very prevalent, the yellow strain being much more injurious to the plant than the green strain   It has been demonstrated that a plant affected with the green strain is immune to the yellow strain (Forbes, Mills, and Edgerton, 1937) The practical importance of this discovery in sugar-cane culture has not yet been determined

Fig 142 —A potato plant affected with leaf roll

Potato Leaf Roll (Solanum Virus 14) —Leaf roll is one of the more destructive virus diseases of the potato   It probably occurs in all countries in which potatoes are grown but appears to be more prevalent in some localities than in others   The disease is characterized by a necrosis of the phloem tissues which results in an accumulation of starch in the aboveground parts of the plant.   This is accompanied by a characteristic thickening and upward rolling of the leaves, giving rise to the name "leaf roll" (Fig 142)   In pigmented varieties, the rolled leaves may show

excessive red pigmentation   Because of the interference with normal starch translocation, the tubers are small, and the yields are low

Transmission of Leaf Roll —The infectious nature of leaf roll was first recognized by Quanjer, Lek, and Botjes in 1916 (Quanjer 1920), and its transmission by aphids was demonstrated by Oortwijn Botjes (1920) and Schultz and Folsom (1921)   Since 1921, many investigators have studied the problem of insect transmission of leaf roll, but there is yet considerable uncertainty as to the exact role of certain insects   No one has been able to transmit leaf roll by artificial sap inoculation although it is readily transmitted by grafting

Oortwijn Botjes (1920) reported transmission by *Aphis rumicis* L and *Myzus persicae* Sulz , and Schultz and Folsom (1921) incriminated *M persicae* and *Macrosiphum solanifolii* Ashm   Murphy (1923) presented evidence to show that the plant bug (*Calcoris bipunctatus*) and a leaf hopper (*Typhlocyba ulmi*) were also vectors of the leaf-roll virus   Murphy and McKay (1929) verified transmission by *Macrosiphum solanifolii* and added *Myzus pseudosolani* to the list of vectors   In 1927, Elze reported that seven different species of insects were capable of transmitting the disease, five of which had not been previously incriminated   These five were *A rhamni, Eupteryx auratus, Lygus sp , Psylliodis affinis,* and the larvae of *Tipula paludosa,* the last-named species working below the ground level.

Smith (1929, 1931c) was unable to transmit the virus with *Calcoris bipunctatus, Lygus pabulinus, Eupteryx auratus, Chlorita viridula, Psylliodis affinis,* and *Macrosiphum gei*   Smith (1934, 1937a) maintains that *Myzus persicae, M pseudosolani,* and *M circumflexus* are the chief vectors and that *M persicae* (Fig 143) is the most important of the three   Dykstra and Whitaker (1938) confirmed the efficient transmission of leaf roll by these three species and showed that it was transmitted less efficiently by *Macrosiphum (Illinoia) solanifolii*   The less efficient transmission by the latter species was attributed to the fact that it fed in vascular tissue in less than 50 per cent of the cases observed whereas the three *Myzus* species habitually fed in the phloem   Further careful experimentation will be necessary before these contradictory results can be explained   However it seems that it would be necessary to assume a simple mechanical process in order

to explain the transmission of a virus by so many different kinds of insect   Inasmuch as the leaf-roll virus is not transmissible by artificial sap inoculation, mechanical transmission by all these insects would appear somewhat doubtful   At any rate, we are concerned with a virus that is not transmissible by artificial sap inoculation but is transmissible by several species of aphid   Since it has been demonstrated that there is an incubation period of the virus in *Myzus persicae* of several days, it is probable that dissemination of the leaf-roll virus in this vector is biological
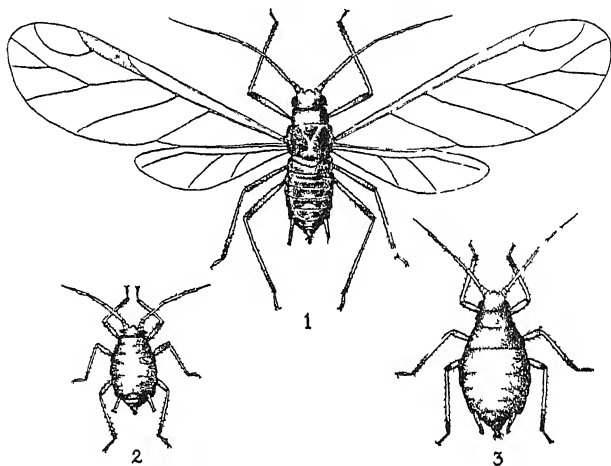
Fig 143 — *Myzus persicae* the vector of leaf roll and more than a dozen other virus diseases   1, adult winged female, 2, immature female 3 adult wingless female   (*After Headlee*)

The fact that the insect retains its infectivity for a relatively long period of time also lends support to this view

The host range of leaf roll has never been studied extensively, but Dykstra (1933) has shown that the virus may be transmitted by *Myzus persicae* from potato to *Solanum villosum*, *S dulcamara*, *Datura stramonium*, and *D tatula* and to the cultivated tomato (*Lycopersicon esculentum*) and that these plants are important carriers of the virus in Oregon

3 TRANSMISSION BY LEAF HOPPERS, BIOLOGICAL AND HIGHLY SPECIFIC

Curly Top of Sugar Beet and Other Plants (Beta Virus 1) — Curly top is one of the most destructive of all virus diseases of plants and probably has been studied more extensively than any

othei similai disease   It is the most destiuctive disease of sugar beets in the iegions wheie it occurs, often causing losses of seveial million dollais in a single season   It is a limiting factoi in beet pioduction in many otherwise suitable iegions   Cuily top is known only in the westein pait of Noith Ameiica, although a similai disease has been ieported from South Ameiica (Fawcett 1927)   Theie is some question of the identity of the South Ameiican virus with that of Westein Noith Ameiica

Cuily top has been observed since 1899, only a few yeais aftei the beet-giowing industry became well established in Ameiica   It was not until the woik of Ball (1906) that the disease was associated with infestations of the leaf hopper (*Eutettix tenellus* Bakei)   The virus natuie of the disease and the iole of the leaf hoppei (*E tenellus*) in tiansmitting the disease weie thoroughly established by the woik of Shaw (1910), Smith and Bonquet (1915), and Ball (1917)   Foi many yeais, the disease was assumed to be limited to the sugar beet and a numbei of native weeds, but the known host iange gradually has been extended (Caisnei 1919, Carsner and Stahl 1924, McKay and Dykstra 1927, Severin and Hendeison 1928, Severin 1929, 1934), until it includes many vegetable and oinamental plants as well as numei-ous species of wild plant   The natuie and prevalence of the other hosts have been shown to have much influence on the epiphytology of curly top on sugai beets

The symptoms of curly top vary with the host plant affected, and on sugar beets they fiequently have been confused with symptoms caused by othei agencies   An extensive and detailed desciiption of the disease on sugai beets has been published by Seveiin (1929), who also pointed out othei abnoimalities that often weie confused with cuily top   Only a veiy brief desciiption will be given heie

The eailiest symptoms appeai as an inwaid iolling of the lowei and outer margins of the youngest leaves (Fig 144) Latei, the entire leaf blade cuils upwaid along the mid-iib Neaily always theie is a distinct clearing of the smaller veins of the leaves associated with the cuiling   The veins aie thickei than noimal and moie or less distoited   a condition that gives a rough warty appearance to the undeiside of the leaf   Affected plants are always stunted, and if infection occurs while the plant is veiy young, it will die prematurely

There is an excessive development of the small fibrous roots, producing the condition often referred to as "hairy" or "wooly" root   The sugar content of affected beets is abnormally low, and the total yield is often negligible   A necrosis of the phloem tissues is the most characteristic internal symptom, and, in severely affected plants, an exudate escapes from the necrotic phloem in the form of brown droplets on the surface of the veins When roots of affected plants are cut in cross section, the necrotic phloem shows as concentric rings of darkened tissue

Fig 144 —Curly top of sugar beet   (*After Severin*)

There are many other occasional and accessory symptoms that are modified by various factors   According to Severin, the most reliable diagnostic symptoms of curly top on sugar beets are "the clearing or transparency of the minute veins on the youngest or innermost leaves in the early stages of the disease and the wart-like protuberances on the lower surface of the leaves in the later stages of the disease

Transmission of Curly Top—Curly top can be transmitted with difficulty by artificial sap inoculation, infection having been secured in a very small percentage of trials (Severin 1924, Carsner and Stahl 1924)   The beet leaf hopper (*Eutettix tenellus* Baker)

(Fig 145) is the only known insect vector   Another species of
leaf hopper (*Agallia sticticollis* Stal) is the vector of a disease
of sugar beets in Argentina which is thought by some to be identi-
cal with curly top   This insect, however, has not been reported
in North America   According to Severin and Henderson (1928)
E tenellus does not occur in Argentina

The transmission of the curly-top virus by *E tenellus* is specific
and biological   The beet leaf hopper is not known to transmit
any other virus, and no other insect is known definitely to trans-
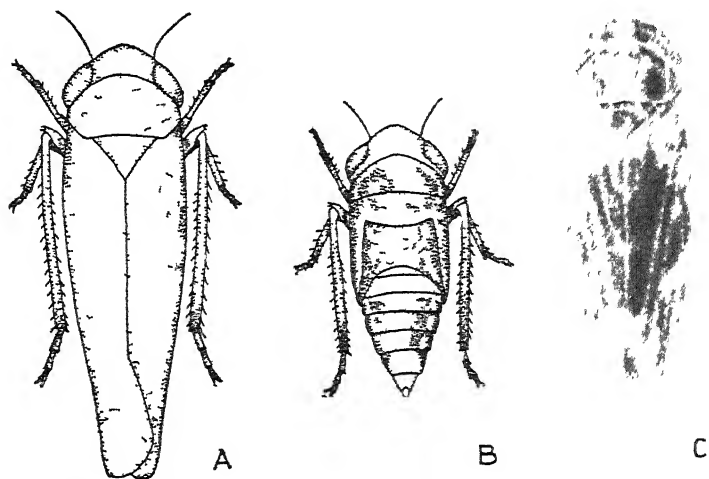
Fig 145 —The beet leaf hopper *Eutettix tenellus* the vector of curly top   *A*
adult, *B*, nymph, *C*, adult   Approx 25 ×   (*A and B after Ball C after Severin*)

mit curly top   There is a distinct incubation period of the
virus in the body of the insect   The minimum incubation period
first was reported as being several hours, but this has been
shortened to 20 minutes when 20 to 50 viruliferous insects are
used   When only 1 insect is used the minimum incubation
period is 7 hours   The latent period of the disease in the plant
varies from 4 to 14 days

The virus of curly top may survive the winter in a number of
wild plants   The weeds in which the virus survives the winter
are those on which the hopper feeds in late fall and early spring
The virus can survive also in overwintered sugar beets in the
field from which it is transmitted to the new crop of seedlings

The available evidence (Wallace and Murphy 1938) indicates that leaf hoppers that hibernate on infected sugar beets transmit a more virulent strain of the virus than is transmitted by those that overwinter in the deserts on wild plants

The fate of the virus in the body of the insect vector has been studied by Freitag (1936) and by Bennett and Wallace (1938) The virus may be recovered from the blood, the salivary glands, feces and the contents of the alimentary tract of viruliferous leaf hoppers It is recovered most readily from the blood, a fact indicating that the blood is the chief reservoir of the virus in the insect The virus content of the insects as well as their ability to transmit the virus decreases slowly over a period of 8 to 10 weeks when they are confined to immune plants Viruliferous leaf hoppers, having fed for 6 hours on virus extracts, lose the power of transmitting the virus after 54 days, when transferred daily on small beet plants, but regain it after feeding for short periods on infected beets These results indicate that the virus does not multiply in the body of the vector It has been shown, however by Wallace and Murphy (1938) that the virus can survive the winter in the body of leaf hoppers without any apparent change in virulence

Swezy and Severin (1930) reported the presence of Rickettsia-like microorganisms in the epithelium and lumen of the intestinal tract of infective leaf hoppers and suggested a possible relationship with the virus There is not sufficient evidence, however, to justify the conclusions that the microorganisms are concerned in the etiology of the disease

The virus is not transmitted through the seed of the sugar beet Although it invades the external tissues of the seed, it does not reach the embryo and when the seeds germinate the seedlings do not become infected The virus is not transmitted congenitally through the eggs of the leaf hopper as shown by the mating experiments of Bennett and Wallace (1938)

Leaf hoppers may be made viruliferous by feeding them on extracts from infected plants A quantity of juice is expressed from tissue and precipitated with an equal volume of 95 per cent alcohol The precipitate contains a high percentage of the virus It is then centrifuged, washed in 50 per cent alcohol, dried, and mixed with a 5 per cent sugar solution equal to the original volume of the juice This in turn is centrifuged, and the super-

natant liquid is used to feed nonviruliferous leaf hoppers through
a suitable membrane   This technique perfected by Bennett
(1935), has been used by Bennett (1934 1937) and by Bennett
and Esau (1936) in extensive studies of the occurrence of the
virus in different tissues and its movement within the plant

The localization of the virus in the phloem of affected plants
is significant in view of the fact that the leaf hoppers feed almost
exclusively upon the phloem tissues and must do so in order to
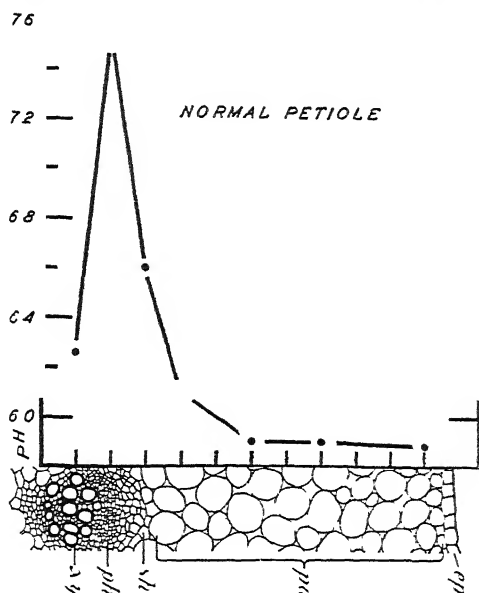
FIG 146 —Diagram showing the pH gradient in a normal sugar-beet petiole
Note that the phloem is more alkaline than the surrounding tissues   xy, xylem
ph phloem, sh bundle sheath pa parenchyma ep, epidermis   This differential
aids the leaf hopper in locating the phloem   (After Fife and Frampton)

ensure infection   A plausible explanation of the means by which
the leaf hoppers are able to locate the phloem has been offered by
Fife and Frampton (1936)   With the aid of a quinhydrone
microelectrode these workers determined the pH value of the
sap of the various tissues of the beet leaf   It was found that
the reaction of the phloem tissue of a normal petiole was approxi-
mately pH 7 5, that of the xylem was about pH 6 2, and that of
the surrounding parenchyma tissue was slightly less than pH 6 0
(Fig 146)   There is therefore a pH gradient between the phloem

and the surrounding tissues   The fact that the saliva of the leaf
hopper is alkaline, approximating that of the phloem, led to the
hypothesis that the pH gradient is used by the vector in locating
the phloem   This hypothesis is supported by feeding experi-
ments in which hoppers showed preference for the alkaline
solutions   Moreover, when beets are subjected to high concen-
trations of carbon dioxide, the pH gradient is disturbed so that

A- CO₂-TREATED PETIOLE

B- RECOVERED PETIOLE

AFTER CO₂ TREATMENT
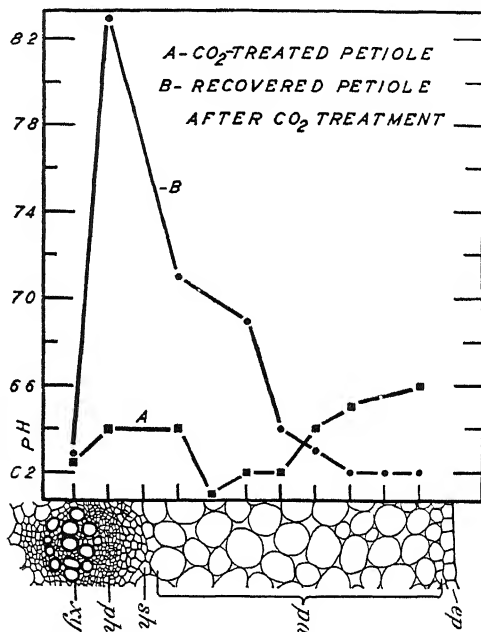
Fɪɢ 147 —Diagram showing the pH gradient in a sugar-beet petiole treated
with carbon dioxide   The differential between phloem and surrounding tissue
has been lost   The leaf hoppers have difficulty in locating the phloem in treated
petioles   (*After Fife and Frampton*)

the hoppers are unable to locate the phloem and feed indiscrimi-
nately on any of the tissues (Fig 147)

    The leaf hopper hibernates in the adult stage chiefly as ferti-
lized females   The males rarely overwinter   The hibernation
is incomplete, there being a rest period without true dormancy
Overwintering occurs chiefly on weed hosts in the arid foothills
surrounding the irrigated beet fields   They overwinter to a
lesser extent in and near old beet fields   Oviposition begins
about Apr 1 on the wild hosts, the most important of which are

the mustards [*Sophia sophia* L , *S filipes* (Gray) Holler, *Sisymbrium altissimum* L], the Russian thistle (*Salsoa pestifer* A Nels), red orache (*Atriplex rosea* L), and the cut-leaf nightshade *(Solanum triflorum* Nutt) There are three generations, or broods, the first of which occurs on the weed hosts The second and third broods develop on sugar beets The size of the third brood varies greatly with weather conditions When the beet crop is harvested, the third brood of hoppers migrates back to the desert foothills

The beet leaf hopper survives only in an arid climate and according to Carter (1930) has probably reached the limit of its spread in North America Because the curly-top disease is dependent upon the vector for its spread, it is limited to the region occupied by the leaf hopper

The optimum conditions for the development of the leaf hopper are those found in a sparse stand of the Russian thistle In heavy stands, the humidity is sufficiently high to check the development of the insect Optimum conditions are approached in beet fields only when the stand is poor or when so heavily infested with curly top that the plants are small Thus the virus transmitted by the insect is of benefit to the vector by ensuring a proper environment in the beet fields If it were not for the effect of the virus on the beets, the beet fields would not be a favorable place for the hoppers to develop

This fact has a practical value in the control of the disease Early planting so that the beets have made good growth by the time the hoppers arrive materially reduces the severity of the injury from curly top The hoppers start migrating to the beet fields when the weed hosts begin to dry up as the dry summer season advances The time of migration may vary in different years and may influence the severity of the outbreaks of curly top Wallace and Murphy (1938) have reported a close correlation between the stage of development of the sugar beets at the time of hopper migration and the amount of damage done They consider this the most important single factor influencing the severity of curly-top outbreaks

Carter (1930) has made an extensive study of the ecology of the beet leaf hopper in which the influence of various factors on the survival and migration of leaf hoppers was evaluated As a result of these studies, a method was developed by which

the probable abundance of leaf hoppers can be predicted with a fair degree of success in early spring before the beets are planted By modification of planting practices according to the predictions, considerable losses can be avoided   Unfortunately, the predictions have not been 100 per cent correct   There are so many unknown factors (collectively termed the biological X) that the predictions are sometimes completely wrong   The prediction practice, at its best, is only an emergency measure

A more promising outlook for eventual reduction of the losses from curly top is offered by the investigations of Piemeisel (1932), Piemeisel and Chamberlin (1936), and Piemeisel and Lawson (1937)   These workers have shown that the population of leaf hoppers has been increased greatly in recent years by the increase of the weed hosts that thrive on abandoned farm lands and in overgrazed pasture land   During and shortly after the World War, when wheat prices were high, much of the marginal dry land was plowed up and sown to wheat   Following the drop in prices, much of this area was abandoned or farmed only intermittently, a great increase in weeds resulted, consisting principally in the preferred weed hosts of the beet leaf hopper Other localities in the beet-growing regions are consistently overgrazed, a factor also favoring certain preferred weed hosts   It was shown that, when the land is not plowed or grazed, it will revert to its natural cover of plants that are not favorable hosts for the leaf hopper   Such protected land, according to these workers, will not produce economically significant numbers of leaf hoppers   They conclude that "the beet leaf hopper and curly top can be controlled provided that all lands not continuously farmed and well farmed can be restored to and maintained as good desert range   Unless present practices are corrected, an increase of weedy areas, leaf-hopper populations, and curly top can be expected "

Another promising method of control of curly top of sugar beet is offered by the development of resistant varieties of sugar beets The Division of Sugar Plant Investigations of the U S Department of Agriculture has introduced several new varieties of sugar beets that are fairly resistant to the disease (Owen *et al* 1939)

With the increased use of resistant varieties and with better control of the leaf hoppers through improved range practices in sugar-beet-growing regions, the outlook for practical control of

this destructive disease is very promising   Efforts to control the beet leaf hopper by intensive spraying practice have not been successful (Douglas, Wakeland, and Gillett 1939)

Aster Yellows (Callistephus Viruses 1 and 1a) —Aster yellows was first recognized and described as a destructive disease by R E Smith in Massachusetts in 1902   Smith was unable to find a fungus or bacterium associated with the disease and expressed the opinion that it belonged to the then little known group of virus diseases   Aster yellows along with many other diseases of ornamental plants received very little attention until many years later   In 1926, Kunkel published results of the first thorough study of the disease   The papers of Kunkel (1926, 1931, 1932, 1937) and Severin (1929, 1932, 1934*a, b*) form the chief source of our information about aster yellows and the relationship of insects to its spread and development

Aster yellows is not limited to asters but has a very wide host range (Kunkel 1931), affecting nearly two hundred species of plants in more than thirty different families   The disease apparently is of American origin and is found throughout North America   It is rare or absent in Europe   A few reports of its occurrence in other countries have appeared in recent years (Fukushi 1930, Ogilvie 1927, Richter 1936)   No accurate estimates can be given of its economic importance, but it is a limiting factor in aster culture in practically all sections of North America and because of its wide host range must be ranked as one of the more destructive diseases

The symptoms caused by the aster-yellows virus vary considerably with the plant affected   Partial chlorosis, resulting in a yellowing of normally green tissues, is the most universal symptom   There is no mottling or mosaic pattern   A clearing of the veins of affected leaves is common   Infected plants are always stunted and often distorted, the degree depending upon how early the plant becomes infected   An excessive branching and shortening of the internodes is often observed (Fig 148) Necrosis occurs in advanced stages, and seed produced on affected plants usually will not germinate   On asters, excessive numbers of trichomes often are formed, and a greening of the petals is not unusual   The roots show no abnormal symptoms

There are several strains of the aster-yellows virus   Severin (1932) and Kunkel (1932) have shown that the virus prevalent in

California will infect celery whereas the one prevalent in New York will not. Severin later (1934a, b) discovered other differences between the two strains of the virus. Kunkel (1937) also reports the isolation of mild strains of the virus by subjecting viruliferous leaf hoppers to high temperatures. The eastern strain of the virus, according to Kunkel (1931), does not affect

Fig 148 — Aster yellows   A, an aster plant affected with yellows, B, a healthy plant of the same age   Note the excessive axillary branching and more erect growth of the leaves and branches of the affected plant   The yellow color of the diseased plant is not shown in the picture   (*After Jones and Riker*)

potatoes, but Severin and Haasis (1934) successfully inoculated potatoes with the California strain   Affected potato plants have slender purple shoots and form aerial tubers in the axils of the leaves   The incubation varied from 20 to 63 days, and the virus was not recovered from infected plants or from tubers produced by infected plants   Naturally infected plants were not observed in the field

Transmission of Aster Yellows —Aster yellows cannot be transmitted by artificial sap inoculation but may be transmitted by grafting   In nature, it is transmitted primarily by a single species of leaf hopper (Fig 149)   There has been some difference of opinion as to the identity of the insect   Kunkel (1926) stated that it "was identified by several authorities to which it was submitted as *Cicadula sexnotata* Fall "   Dorst (1931, 1937), however, claims that *C sexnotata* is the European species and is not found in America   The American species, according to Dorst, is *Macrosteles divisa* (Uhl) (*C divisa* Uhl) Kunkel (1926) reported that specimens had been submitted to the British Natural History Museum in London and that Mr China noted slight differences in color markings but considered the British and American insects as belonging to the same species

Kunkel (1926), after considering evidence submitted by various entomologists, concluded that the insect is an introduced species and that "it seems probable that it was introduced into this country less than 100 years ago "   If we accept this conclusion, we are faced with the problem of explaining the origin of the disease   If the disease does not occur in Europe, it probably was not introduced into North America with the insect vector   If the vector did not occur in this country 100

Fig 149 —*Macrosteles divisa*, the principal vector of aster yellows   An adult leaf hopper   (*After Severin*)

years ago, how was the virus disseminated before that time?   Is there some still unknown vector, or is the virus of relatively recent origin?   A possible explanation may be offered in the demonstration by Severin (1934*b*) that two other species of leaf hopper (*Thamnotettix montanus* Van D and *T geminatus* Van D) may transmit the virus but not so effectively as the better known vector   However, because of the specific obligate and biologic relationship between the insect and the virus, it seems more logical to assume that the principal and perhaps the original vector is *M divisa* and that it is native to this country

The vector, like the virus it transmits, has a broad host range and is widely distributed throughout North America   It may overwinter in the egg stage, and in the milder climates it may hibernate as adult hoppers   The overwintering eggs are deposited under the epidermis of plants, such as rye, that remain green over winter   There are five nymphal instars   The eggs hatch in 11 to 13 days in summer, and the length of the nymphal period varies from 16 to 30 days   The various generations overlap to such an extent that there are no distinct broods   The insects feed chiefly upon the veins of the leaves   Both nymphs and adults are able to transmit the virus, but an incubation period of at least 10 days in the insect is required before it becomes infective   Therefore, the disease is rarely transmitted by the early nymphal instars   Some individual insects remain viruliferous for their entire life, but others may retain the virus for a short time only   Kunkel (1937) recently has shown that viruliferous insects held at high temperatures (31 degrees centigrade or above) for several days lose the virus and become noninfective   He thinks that the vectors may commonly lose the virus in the hot weather of midsummer, thus accounting for the observed slower spread at that season of the year   Viruliferous individuals appear normal in structure (Dobroscky 1929, 1931), and the virus has not been detected in the body of the insect by histological methods   The virus is not congenitally transmitted through the egg

The latent period of the virus in the plant averages 18 days at normal temperatures   The virus overwinters in susceptible perennial plants such as *Chrysanthemum, Sonchus, Asclepias, Erigeron,* and *Plantago*   It is not transmitted through the seed of the aster   Seeds produced on affected plants usually do not germinate

Aster yellows can be controlled only by protecting the plants from the hoppers   As *M   divisa* is not a natural greenhouse insect, the control of the disease in greenhouses is not difficult   Spraying has not proved effective in protecting the plants from the insect   It is the common practice where the disease is prevalent to grow asters under large cages made of cloth netting or screen wire   This method gives very satisfactory control (Jones and Riker 1931) and is used commercially on an extensive scale

Streak of Corn (Maize) (Zea Virus 2) —Corn (*Zea mays* L)
in Africa is affected with a destructive virus disease known as
"streak " The disease was first described briefly in 1901 by
Fuller   It was recognized as a virus in 1925 by Storey, who has
studied it extensively since that date   It has not been reported
from any locality outside Africa, where it is one of the major
diseases of corn   No accurate figures are available as to the
amount of injury   Storey has reported as high as 100 per cent
infection in certain fields, but much of the disease appears late
in the season, and late infections are less injurious than early ones
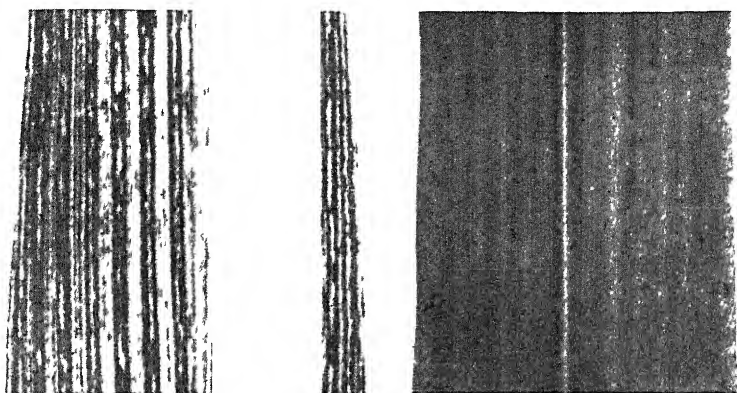
Fig 150 —The streak disease of corn   A portion of a leaf affected with
the disease (left), compared with a similar portion of a healthy leaf   (*After*
Storey)

The symptoms of streak appear first as very small colorless
spots scattered over the leaves   These gradually elongate into
streaks of yellow chlorotic tissue along the veins (Fig 150)
Since the virus is not seed-transmitted, the first leaves often
escape infection until they are fully differentiated and con-
sequently no streaks develop   The host range of streak is not
fully known, but in addition to corn a number of wild grasses
are also affected

The virus is incapable of causing permanent infections on
sugar cane, which appears to be highly resistant   There is a
similar streak on Uba cane, but the latter disease causes only
mild symptoms on maize   Storey considers the two viruses to
be different   Still another virus disease of maize has been
reported by Storey (1937)   This causes a mild mottling of

affected leaves and has been named "mottle" Although the
mottle virus is transmitted by the same insect vectors that
transmit streak, Storey considers it to be unrelated to the streak
virus

Transmission of Streak —The methods of transmission of this
virus have been investigated very thoroughly by Storey (1925,
1926, 1928, 1932a, 1933) The virus is not transmitted through
the seed of the corn plant, and all efforts to transmit it by arti-
ficial sap inoculation have failed It is transmitted with a high
degree of efficiency by the leaf hopper [*Cicadulina mbila* (China)]
and Storey (1937) has recently reported that two closely related
species (*C zeae* China and *C storeyi* China) are also able to
transmit it *Aphis maidis*, the principal vector of sugar-cane
mosaic, *Peregrinus maidis*, the vector of a mosaic of corn in
Hawaii, and about twenty additional species of insects found on
corn are unable to transmit the streak virus The transmission
appears to be biological and specific for the leaf hoppers of the
genus *Cicadulina*

There is a minimum incubation period of the virus in the
vector, varying from 6 to 12 hours at 30 degrees to 84 hours at
16 degrees centigrade The latent period in the corn plant varies
from $3\frac{1}{2}$ to $7\frac{1}{2}$ days in rapidly growing young plants It is
somewhat longer in older plants, depending on the temperature
and the part of the plant inoculated

The leaf hopper may acquire and transmit the virus as either
nymph or adult but does so more readily as a nymph After
the virus has been acquired by the nymph, the insect retains it
for the rest of its life The virus can be acquired by feeding for
1 hour on an infected plant, but greater success results from
somewhat longer feeding periods One insect is sufficient to
transmit the virus, but a higher percentage of infection is often
obtained when several insects are used

Infection follows feeding by viruliferous leaf hoppers on either
young or old tissues Symptoms appear sooner if young leaves
are inoculated and may not appear at all on the older parts
although the younger tissues of the same plant will show them
The virus travels down the leaves from the point of inoculation
and up the stem until the growing point is reached The rate
of travel varies considerably, but it may be as fast as 40 centi-
meters per hour The virus is localized in certain tissues of

infected plants When the leaf hoppers are fed on the normal green areas of the leaf, they do not acquire the virus It can be acquired only by feeding on the yellow tissues

The virus is filterable through Chamberland *L*1 filters, Berkfeld *v* and *n* filters, and to a slight extent through Chamberland *L*3 filters but will not pass a Seitz E K filter disk When insects are fed through membranes on the filtered juice, they become viruliferous

Certain individual leaf hoppers appear never to become viruliferous even though they may feed indefinitely on infected plants This phenomenon has been investigated by Storey (1932a, 1933), who has shown that the ability or inability to become viruliferous is an inherited character, being inherited as a dominant sex-linked character An individual insect that is unable to transmit the virus is said to be "inactive", one that is capable of transmitting the virus is "active" When an active female is crossed with an inactive male the F_1 progeny is entirely active The F_2 progeny of this cross consists of active females and both active and inactive males When inactive females are crossed with active males, the F_1 progeny consists of active females and inactive males Both active and inactive males and females appeared in the F_2 progeny of this cross These results support the hypothesis that the male insect is heterozygous for sex and that the factor for activity is dominant to that of inactivity and linked with sex

Storey (1933) made an exhaustive study of the mechanism of transmission of the virus by *C mbila*, and his results throw considerable light on the question A technique was devised by which insects could be made viruliferous by injecting the virus obtained from viruliferous insects into the body cavity of other insects With the aid of this technique, a study was made of the distribution of virus in the body of the vector The virus was detected in the contents of the rectum of viruliferous or active insects provided that the insect had recently fed upon a diseased plant It was not found in naturally voided feces The virus was always present in the blood of viruliferous individuals, and it could be detected in the blood before the normal incubation period had elapsed The virus could be demonstrated in the rectum of inactive insects that had recently fed on diseased plants but was never found in the blood of such insects Inactive

individuals were made active by injecting the virus into the blood
When inactive insects that had recently fed on infected plants
were punctured with a very fine sterile needle, they became
viruliferous, provided that the needle had punctured the intes-
tinal tract   *Peregrinus maidis* and *A maidis* could not be made
viruliferous by inoculation

These results led Storey to conclude that the virus normally
enters the intestine through the mouth, diffuses through the
intestinal wall into the blood, and from the blood passes into the
salivary glands, from which organs it is introduced into the plant
during feeding   He concludes that the inability of the inactive
leaf hopper to transmit the virus is caused by the impermeability
of its intestinal wall to the virus   On the basis of this conclusion,
the incubation period in the insect could be interpreted as the
time required for the virus to diffuse through the intestinal wall,
reach the salivary glands, accumulate there in sufficient quantity,
and be passed out in the saliva

Storey (1937) has reported, from East Africa, another virus
that affects corn, causing a transitory, diffuse mottling on the
leaves   The mottle virus is transmitted by *C mbila, C zeae*, and
C storeyi, which are also the vectors for streak   Those races of
C mbila which are unable to transmit the virus of streak usually
are likewise unable to transmit the mottle virus although there
are a few exceptions   The virus is not transmitted by artificial
sap inoculation   The presence of one virus in the plant does not
inhibit the development of the other, and the presence of one
virus in the insect does not prevent it from transmitting the other
although one virus may cause a slight delay in the development
of symptoms by the other

The Dwarf (Stunt) Diseases of Rice (Oryza Virus 1) —The
dwarf disease of rice is of particular historical significance because
it is the first plant virus disease shown to be transmitted by an
insect vector   Takami, in 1901, reached the conclusion that the
dwarf disease was caused by the feeding of the leaf hopper
(*Nephotettix apicalis* Motsch var *cincticeps* Uhl)   According
to Katsura (1936), Takami did not conceive of the insect as the
vector of a virus but as the direct cause of the disease   It was not
until 1908 and 1909 that the virus nature of the disease and the
true role of the leaf hopper as a vector were established independ-
ently by workers at two different experiment stations in Japan

Fukushi (1937) who has shown that the leaf hopper (*Deltocephalis dorsalis* Motsch) also is a vector of the disease has pointed out that Takata, as early as 1895, claimed that this insect was responsible for the disease
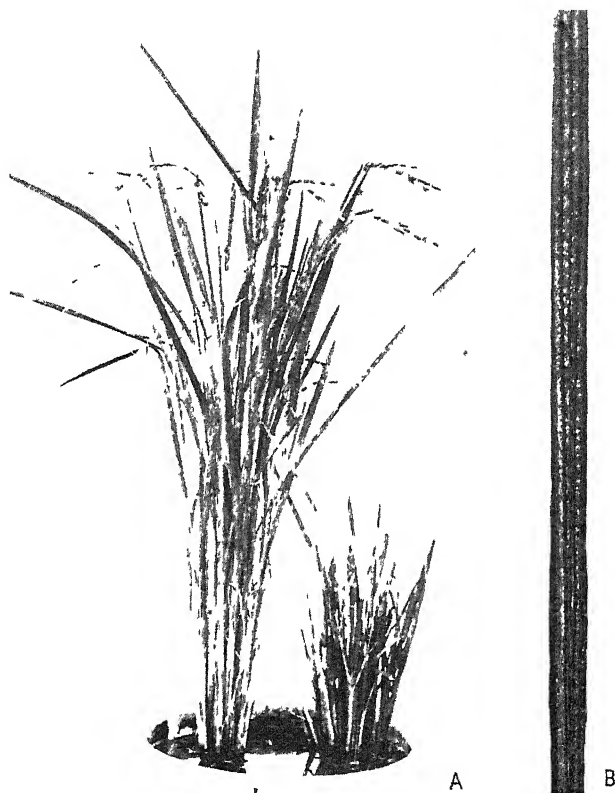
FIG 151 —Rice dwarf   *A*, a healthy plant and a diseased plant growing in the same pot, *B*, a single rice leaf showing the interrupted chlorotic streaks that are characteristic of affected plants   (*After Fukushi*)

Dwarf of rice has been destructive in Japan for many years Katsura reports historical records of famines caused by rice failures as early as 1773 and attributes the failure to the dwarf disease   More recent crop failures since 1883, involving famine and many deaths, can be attributed definitely to dwarf   The disease has not been reported from any other country

The symptoms have been described in detail by Fukushi (1934*a*) who has done the best of the more recent work on the

disease   As the name indicates, there is a marked stunting of affected plants, accompanied by a correspondingly reduced yield of grain (Fig 151)   The first symptoms usually appear in late June after the plants have been transplanted into the fields and when they are 6 to 8 inches high   Small chlorotic spots appear along the veins of the new leaves   The spots gradually elongate, forming continuous or interrupted streaks parallel with the veins Root development is arrested, and few or no fruiting panicles are formed, depending upon how early the plant is infected

In addition to rice, the disease affects the following plants (Fukushi 1934*b*) *Panicum miliaceum* L , *Echinochloa crus-galli* Beauv subsp *colona* var *edulis* Honda , *Poa pratensis* L , and *Alopecurus fulvus* L   Rye, wheat, and oats are slightly susceptible, but corn, Italian millet, barley, and sorghum are not infected

Transmission of the Dwarf Disease of Rice —The leaf hoppers (*Nephotettix apicalis* Motsch var *cincticeps* Uhl and *Deltocephalus dorsalis* Motsch) are the only known vectors of the virus   The disease is not transmissible by mechanical sap inoculation or through the seed of rice   There is no evidence of transmission through the soil

Our knowledge of the transmission of the virus of rice dwarf is based almost entirely on work done with *N apicalis*, the other vector having been studied very little   Transmission by the leaf hoppers apparently is biological   An incubation period in the insect body is necessary although the minimum time is variable and has not been definitely determined   A minimum feeding period of 3 days is necessary for a nonviruliferous leaf hopper to pick up the virus   Some individuals do not become viruliferous even after prolonged feeding on infected plants

The vector (*N apicalis*) (Fig 152) is of particular interest because in it the virus is transmitted from one generation to the next congenitally through the egg   Fukushi (1933, 1939) has shown by crossing experiments that transmission through the egg occurs only when the female parent is viruliferous   In other words, when noninfective females are crossed with infective males the virus is not transmitted to the progeny, but, on the other hand, when infective females are crossed with noninfective males a relatively large percentage of the progeny are infective (see Table II)   Fukushi believes that the eggs become infected in the early stages of their development in the ovary, but appar-

ently some of the ova may escape infection   This is the only
known example of the congenital transmission of a plant virus
Transmission of the virus through the egg was proved by picking
up the nymphs bred from infective female leaf hoppers as soon
as they hatch and before they have had time to feed on the
infected plant and transferring them to healthy plants   Con-
genital transmission was demonstrated for seven successive
generations in experiments reported by Fukushi in 1939

There are four to five broods of the leaf hopper (*N apicalis*)
It usually overwinters as nymphs feeding on *Astragalus sinicus* L
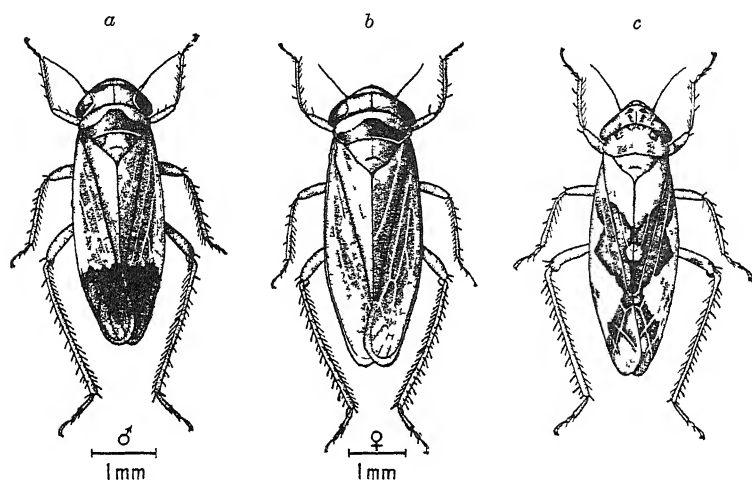
Fic   152 —The vectors of rice dwarf   *a* and *b*   *Nephotettix apicalis* var
cincticeps Uhl , *c, Deltocephalis dorsalis* Motsch   (*Illustrations by courtesy
of T Fukushi*)

and wild grasses, and matures in April or May   Twenty-seven
to thirty-three days are required for the completion of a life cycle
The virus may live over winter in multiferous nymphs or in
susceptible perennial hosts   *Alopecurus fulvus* and *Astragalus
sinicus* L are potential overwintering host plants, but it has not
been proved definitely that the virus survives in either of them
Fukushi (1934*a*) states that effective control of the dwarf disease
is being accomplished by controlling the leaf hoppers

Peach Yellows (Prunus Virus 1) —Peach yellows has been
recognized for more than a hundred years as one of the most
destructive diseases of peaches   The disease is found only in
North America and appears to be limited to the eastern part of

the continent, extending westward through the upper Mississippi
Valley and Great Lakes region to the Mississippi River   The
host range of the virus is not fully known, but Smith (1888)
states that it affects "peaches, nectarines, almonds, and apri-
cots "   Manns (1933, 1934, 1935, 1936) and Manns and Manns
(1935) have shown that the wild plums (*Prunus myrobalan* and
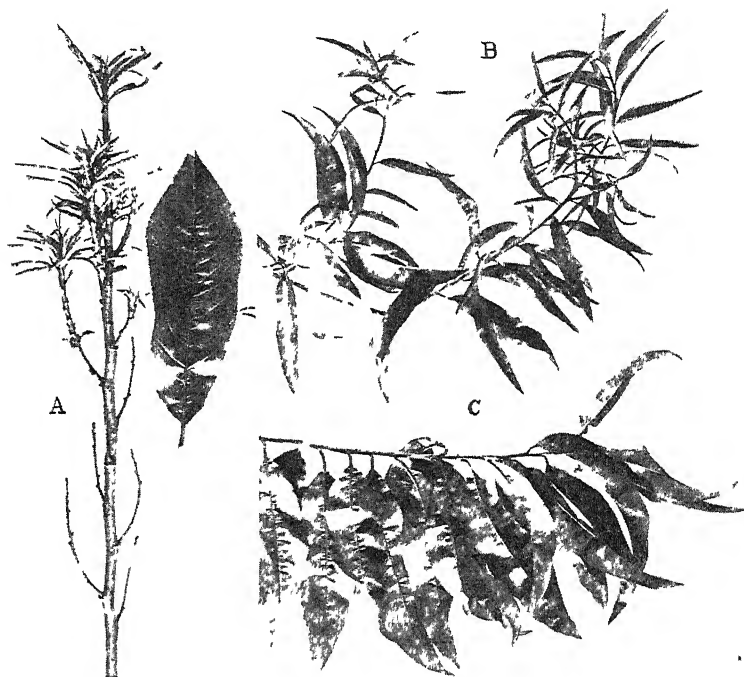
Fig 153 —Peach yellows   *A*, a typical infected shoot showing the upright
habit and small narrow yellow leaves with a normal leaf for comparison, *B*, a
terminal shoot infected with yellows, *C*, a healthy terminal   (*After McCubbin,
Pennsylvania Dept Agr Bul* 382)

P munsoniana), the wild peach (*P persicae*), and the Japanese
plum (*P salicina*) are carriers of the virus
    The disease is characterized by small pale yellow leaves borne
on slender excessively branched twigs that tend to grow more
erect than normal, forming a so-called "witches'-broom "   (Fig
153)   The leaves may droop and curl upward and inward along
the margins   The fruit on affected trees ripens prematurely
and is often speckled or blotched with red   The texture of the

fruit is watery, and the flavor is insipid   An infected tree never recovers and may serve as a center of infection for further spread

Transmission of Peach Yellows —Smith, in 1888, was the first to demonstrate the infectious nature of the disease   He proved that it was transmitted by grafting or budding but not by direct sap inoculation   He was unable to discover the method of spread

Fig 154 —*Macropsis trimaculata*, the vector of peach yellows   (*After Kunkel by courtesy of the Boyce Thompson Inst Plant Research*)

in nature, and this aspect of the problem has defied the efforts of many capable investigators since 1888

In 1933, Kunkel demonstrated that the vector of peach yellows is the plum leaf hopper [*Macropsis trimaculata* (Fitch)] (Fig 154)   Unsuccessful attempts to transmit the virus were made with the following species of insects   *Myzus persicae* (Sulz), *Aphis persicae-niger* Smith, *Lygus pratensis* (L), *Conapsis*

eutosa Say, *Pseudococcus citri* Risso, *P longispinus* (Targioni),
Philaenus leucothalmus (L) var *pallidus* (Zett), *Thelia trima-
culata* (Fabr), *Graphocephala coccinea* (Forst), *Empoa rosae* (L),
Jassus olitorius Say, *Freberiolla flori* (Stal), and *Erythroneura
obliqua* Say   Manns (1935, 1936) has failed to transmit the virus
with *Ceresa bulbatus* Fabr, *Gypona octolineata* var *striata*
Burm, *Thelia uhleri* Stal, *Phlepsius irroratus* Say, *Ascanolonia
conica* Say, *Ormensis pruinosa* Say, and *Cicada septendecim* L
Hartzell (1935) tested 48 different species of insects and was
unable to transmit the virus with any except *M trimaculata*
Inasmuch as the insects tested include the most common sucking
insects found on the peach in the region where yellow occurs, it
is likely that *M trimaculata* is a specific and obligate vector of
the disease

Peach yellows is not transmissible by artificial sap inoculation,
according to the work of Blake, Cook, and Connors (1921),
Manns (1924), Hartzell (1935), and several other investigators
Although occasional claims of seed transmission have been made,
the evidence clearly indicates that it is not transmitted either
through the seed or through pollen

The discovery of the vector of peach yellows may prove very
significant in the practical control of the disease   As pointed
out by Hartzell (1935), *M trimaculata* produces only one genera-
tion a year, and any individual leaf hopper killed would not be
replaced during the current season   The population trend of
the insect on wild plum and peach in New York in 1934 is given
in Fig 155   The nymphs are not so active as most species of
jassids and should be relatively easy to kill by contact sprays
Manns (1934, 1935) has demonstrated that *M trimaculata*
transmits the virus of "little peach" as well as that of peach
yellows

The percentage of success in transmitting the virus of peach
yellows with *M trimaculata* has always been relatively low, a
fact indicating that all individuals may not be capable of trans-
mitting it   The length of the incubation period in the insect has
not been definitely determined, but it may vary from 8 to 26
days (Hartzell 1936)   Both nymphs and adults are able to
acquire and transmit the virus   Intracellular inclusions have
been demonstrated in the intestinal walls and in the salivary
glands of viruliferous leaf hoppers by Hartzell (1937)

The plum, including wild species, is a favorite host of *M trimaculata*, and being susceptible to yellows it constitutes an important source of infection for peach orchards   The destruction of these breeding places may be of value in the control of the disease   Manns (1934) reported that the Japanese varieties (*Prunus salicina*) are hosts of the vector and that the variety Abundance is a symptomless carrier of peach yellows and little peach   This variety is considered especially dangerous as a source of infection to peaches   Manns has expressed the opinion
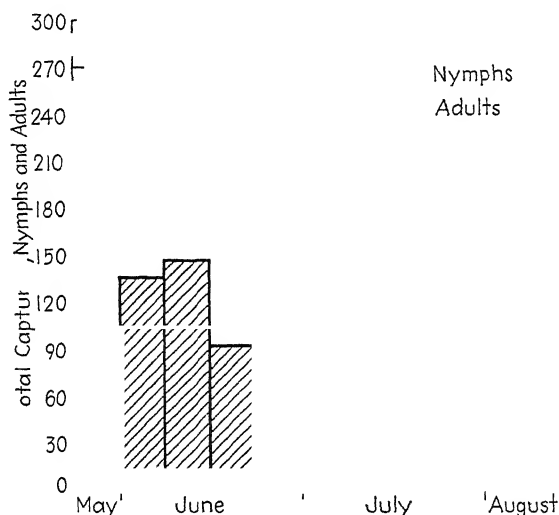
Fig 155 —The seasonal abundance of *Macropsis trimaculata* the vector of peach yellows, at Yonkers, N Y, in 1934   Note that there is only one brood which reaches its greatest numerical abundance during the last week of June (*After Hartzell*)

that the virus of peach yellows may have been introduced into America on the oriental plums

False Blossom of Cranberry (Vaccinium Virus 1) —This destructive virus disease of cranberries was first observed in Wisconsin but is now present wherever cranberries are grown in the United States   It is not known outside North America The disease, as the name indicates, causes a malformation of the blossoms that usually renders them sterile (Fig 156)   The normal floral elements are often replaced by leaflike structures that manifest a variety of abnormal modifications   Axillary buds are stimulated to growth resulting in a witches'-broom effect

The yield of fruit on infected plants is greatly decreased, and fruit that does mature is of inferior quality   A good description of the disease has been published by Dobroscky (1931) who also demonstrated its method of transmission

Transmission of False Blossom —The virus of false blossom has not been transmitted by artificial sap inoculation   It also has not been transmitted by grafting because of the inability to obtain satisfactory graft unions   In nature, it is transmitted

FIG 156 —False blossom of cranberry   *A*, a healthy shoot with normal blossoms,
B, a diseased shoot with sterile blossoms   (*After Beckwith and Hutton*)

by the blunt-nosed leafhopper (*Euscelis striatulus* Fall) (Fig 157) as demonstrated by Dobroscky (1929, 1931)   No other vector is known

The spread of false blossom from Wisconsin through the regions of cranberry production has been rapid   The virus was introduced into new regions on infected plants, and further spread has been effected by the leafhopper vector   An enlightening account of the spread of the disease and the part played by the vector *E striatulus* has been given by Stevens (1930)   The spread of the disease was very rapid in the decade between 1920 and 1930,

a fact attributed in part to the use of more susceptible varieties and in part to an increase in the abundance of the insect vector The increased abundance of the insects was attributed to certain changes in cultural practices that resulted in less effective control of the insects For example, during the period of greatest spread of the disease there was a decrease in the practice of insect control through late flooding of the bogs
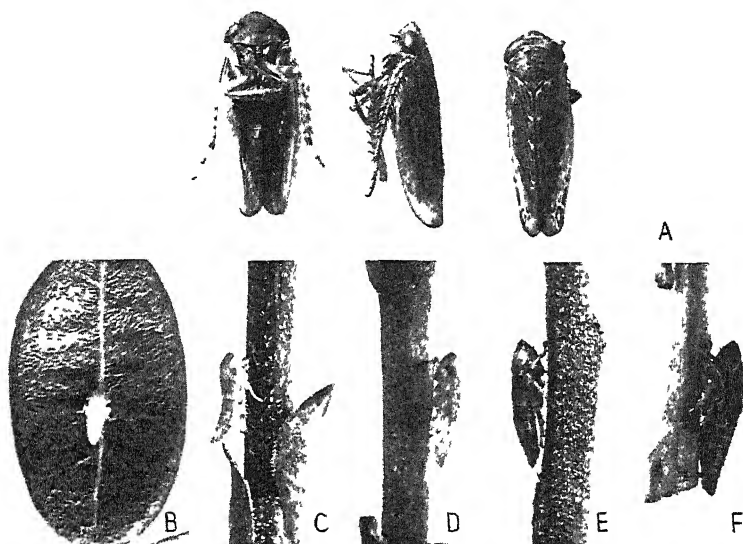
Fig 157 —The blunt-nosed leaf hopper, the vector of cranberry false blossom A, three adults, showing ventral, lateral and dorsal views, B to F, the five successive nymphal instars (After Beckwith and Hutton)

Although false blossom is present in the bogs of the Pacific Coast states where it was introduced on diseased plants, it has spread very little and is of minor importance The failure of the disease to spread in these regions can be explained by the absence of the vector, which has not been found in Western United States

Euscelis striatulus is the most abundant leaf hopper found in cranberry bogs It occurs in small numbers on wild cranberries and related plants, but is most abundant in cultivated bogs There is only one brood each year The eggs are deposited under the bark of the young shoots in August and September, remaining

dormant over winter and hatching in late May or June   There are five nymphal instars, each lasting about seven days (Fig 157) The adults, therefore, are most numerous in July and August The life history of the insect in relation to the false-blossom disease has been studied by Beckwith and Hutton (1929)

Control of false blossom is being accomplished largely through the growth of resistant varieties such as McFarlin and through better control of the insect vector   The most practical method of doing this is by flooding the bogs in late June just after the eggs have hatched, but since some injurious effects have followed

Fig   158 —Potato yellow dwarf   Two plants showing symptoms of different degrees of severity   (*Photographs by courtesy of the Wisconsin Agr Exp Sta*)

flooding at certain times, further studies in control are desirable Some success has been obtained by spraying in late June with pyrethrum sprays (Beckwith and Hutton 1929)

Potato Yellow Dwarf (Solanum Virus 16) —Yellow dwarf was first recognized in 1917 in New York and was described by Barrus and Chupp in 1922   The disease is now known to be present to some extent throughout the northeastern part of the United States   It has not been reported from outside continental North America   It is not uniformly distributed but appears to be very destructive in certain local regions and absent in others

The symptoms of yellow dwarf vary extensively (Fig 158) Black (1937) recognized two distinct types of symptom, referred

to as acute and chronic   The acute symptoms are found on newly inoculated plants and consist of extreme dwarfing caused by the death of the apical meristem, accompanied by pronounced yellowing of the leaves   There is an apical internal necrosis of the stem and a necrotic spotting of the internal tissues of the tubers   The chronic symptoms appear later after a state of equilibrium between virus and suscept has been reached   They consist of a spindly growth with slightly mottled and ruffled leaves   The necrosis of apical meristem and the extreme dwarfing are absent   The virus is not attenuated in the chronic stage, as proved by the acute symptoms that develop when healthy plants are inoculated by grafting with plants showing the chronic symptoms

The symptoms are strikingly modified by temperature, as shown by Goss and Peltier (1925), Black (1937), and Walker and Larson (1938 and 1939)   The symptoms are most acute at the higher temperatures (24 to 28 degrees centigrade)   At soil temperatures of 16 degrees centigrade, the symptoms are almost entirely masked

Fig   159 —The clover leafhopper (*Aceratagallia sanguinolenta*), the vector of potato yellow dwarf $8^1{}_2 \times$ (*After Black*)

Transmission of Yellow Dwarf —This disease is transmitted by grafting and by insects, but it has not been transmitted by direct sap inoculation   The virus is perpetuated through the tubers of infected plants   There have been some differences of opinion as to the insect vectors of yellow dwarf   Koch (1934) reported transmission by *Myzus persicae* Sulz , and Muncie (1935) claimed that *Macrosiphum solanifolii* Ashm and *Empoasca fabae* Harris are vectors of yellow dwarf   Black (1937), however, has been unable to confirm the work of Koch and Muncie in carefully controlled experiments   Black has presented convincing data that the virus is readily transmitted by the clover leaf hoppers (*Aceratagallia sanguinolenta* Prov) (Fig 159)   He was unable to transmit it with *M persicae, E fabae, Macro-*

siphum solanifolii, Phenacoccus gossypii Towns and Ckl , *Pseudococcus citri* Risso, *Deltocephalus mimicus* Say, *Lygus pratensis* L , and potato flea beetles   The disease has not been found occurring naturally outside the known range of the clover leaf hopper which includes practically all the United States east of the Rocky Mountains   Transmission by the clover leaf hopper has been confirmed by Walker and Larson (1939)

The complete host range of the virus is not known, but the important leguminous hosts of the leaf hoppers are susceptible Black has shown that *Trifolium pratense* L , *T hybridum* L , *T repens* L , and *T agarium* L are susceptible to the yellow dwarf virus

The clover leaf hopper lives over winter in the adult stage and is to be found in clover and potato fields throughout the growing season   Black has shown that the virus is preserved over winter in the body of the vector and that the overwintered vectors may be actively viruliferous   The proximity of clover fields to potato fields in New York has much influence on the epiphytology of the disease on potatoes   Visual evidence of the spread of the virus from clover fields is not uncommon   The virus is not transmitted through the seeds of clover   For this reason the amount of the virus in clover fields increases with the age of the field   Two- and three-year-old fields are more dangerous as infection sources than one-year fields   This relationship between clover fields and yellow dwarf in potatoes was not observed in Wisconsin by Walker and Larson (1939)

The Fiji Disease of Sugar Cane (Saccharum 2) —The Fiji disease has been known for more than thirty years   It was first observed in the British Crown Colony of Fiji from which it has derived its name, and it was first described adequately by Lyon in 1910   It is now known to occur in Australia, the Philippine Islands, Java, and New Guinea where it is one of the major diseases affecting sugar cane

The most characteristic diagnostic symptoms of the Fiji disease are the small elongate galls formed on the veins on the under surface of the leaves   The galls are smooth and lighter green than the normal tissue (Fig 160)   The leaves are distorted, and the entire plant is stunted   It spreads rapidly and often may result in almost 100 per cent loss in a susceptible variety

Transmission of the Fiji Disease —The disease is transmitted vegetatively through sets and ratoons from diseased canes, and recovery has never been observed   It has never been transmitted by artificial sap inoculation   In the field it is transmitted by leaf hoppers of the genus *Perkinsiella*   Proof of its transmission by these insects was obtained independently and at approximately the same time by Ocfemia (1933, 1934) in the Philippines and by Mungomery and Bell (1933) in Queensland, Australia
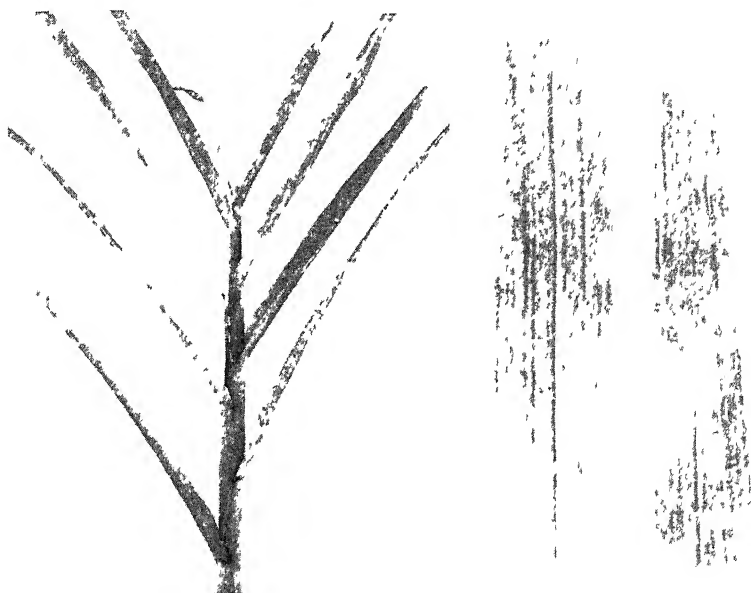
Fig 160 —The Fiji disease of sugar cane   *A*, a single stalk showing the stunted growth and shortened internodes, *B* the long, light-colored elevated leaf galls that are characteristic of the disease   (*Photographs by courtesy of G O Ocfemia*)

In the Philippines the disease is transmitted by *P vastatrix* Breddin and in Queensland by *P saccharicida* Kirk   In the latter case, the disease was transmitted only by the nymphs while in the Philippines, according to Ocfemia, it was transmitted by adult insects   In a later paper, Ocfemia and Celino (1939) reported that the second, third, fourth, and fifth instar nymphs of *P vastatrix* could transmit the virus but the first instar nymphs could not do so   The highest percentage of successful transmission was obtained with the fifth instar nymphs and the incu-

bation period was shorter   These authors also presented
evidence to show that the virus is not congenitally transmitted
through the eggs of *P vastatrix*

The bionomics of the sugar-cane leaf hopper (*P vastatrix*)
(Fig 161) has been studied extensively by Urbino (1927)   Sugar
cane is the only known host of the insect in the Philippines   It
is considered a major pest of this crop   The insect is known only
in the oriental region of the Eastern Hemisphere   Since sugar
cane is an introduced species in the Philippine Islands, Urbino
believes that some native grass served as the primitive host of
the insect

Fig 161 —*Perkinsiella saccharicida*, one of the two known vectors of the Fiji
disease of sugar cane   (*Photograph by courtesy of G O Ocfemia*)

4 TRANSMISSION BY THRIPS, BIOLOGICAL AND SPECIFIC

Spotted Wilt (Lycopersicum Virus 3) —Spotted wilt, a destruc-
tive disease of tomatoes, was first described in Australia in 1919
by Brittlebank   It is considered the most destructive disease
of tomatoes in that country and lately has been reported from
New Zealand (Chamberlain and Taylor 1936), England (Smith
1932), Canada (Berkeley 1935), and from several localities in
the United States (Doolittle and Sumner 1934, Gardner and
Whipple 1934)   The disease is not confined to the tomato but
has a very wide host range, including many weeds as well as
agricultural crops   It is said to be very prevalent on many
species of ornamental flowering plants (Bald and Samuel 1931,
Gardner, Tompkins, and Whipple 1935, Snyder and Thomas

1936)   In respect to host range, the virus is similar to that of
aster yellows and curly top, but it differs strikingly in other
respects

The term "spotted wilt' is, in some respects, a misnomer, as
pointed out by Samuel, Bald, and Pittman (1930), for affected
plants are not always spotted, and they never wilt as a result of

Fig 162 —A tomato leaf affected with spotted wilt   The lower leaflets show the
typical bronze mottled area   (*After Samuel, Bald, and Pittman*)

the disease   The most characteristic symptom on tomatoes is
the sudden appearance of bronze-colored areas on the younger
leaves of rapidly growing plants (Fig 162), followed by an
equally sudden cessation of growth   The detailed symptoms
vary greatly according to the species of plant affected, the
variety, its age, and the prevailing temperature   Plants infected
while very young may die prematurely, but older plants live for

months in a dwarfed condition   In warm weather, excessive
lateral branching may occur, giving the plant a bunchy appear-
ance   Little or no fruit is formed on severely affected plants
Fruit, when produced, ripens slowly and is of poor quality
Often, distinct lesions occur on the fruit in the form of concentric
circles of discolored tissue (Fig 163)   These concentric rings
are the typical symptoms produced by the virus on many other
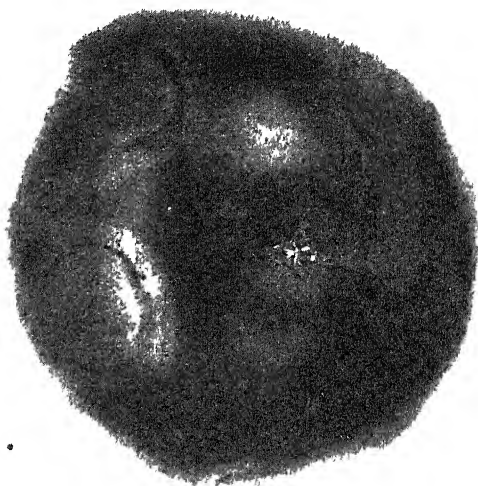
Fig 163 —A tomato fruit affected with spotted wilt   (*After Samuel, Bald,
and Pittman*)

species of plants where the disease has been called "ring spot"
(Smith 1932)

Transmission of Spotted Wilt —Spotted wilt is readily trans-
mitted by artificial sap inoculation, but in nature it is trans-
mitted chiefly by several species of thrips (*Thrips tabaci* Lindeman,
Frankliniella lycopersici,[1] *F occidentalis* Perg , and *F moultoni*
Hood)   Spotted wilt is the first virus disease shown to be trans-
mitted by thrips   Pittman in 1927 presented evidence to show

[1] There has been some question as to the correct identification of this
insect   It was first identified as *F insularis* Franklin, but Steele (1935)
concluded that it was a new but unnamed species   It was finally identified
as *F lycopersici n sp* by Andrewarther (1937)

that the disease is transmitted by *T tabaci*, and in 1930 Samuel, Bald, and Pittman showed that *F lycopersici* is an effective vector These authors concluded that *T tabaci* was not a true vector and that perhaps Pittman's identification had been erroneous Smith (1932), however, proved that *T tabaci* is an effective vector in England, and now both insects are recognized as vectors in Australia (Bald and Samuel 1931) *Frankliniella occidentalis* and *F moultoni* have been reported as vectors of the disease in California (Bailey 1935, Essig and Michelbacher 1936) Many other insects have been tested, but the thrips are the only vectors known

Even though the disease may be transmitted by artificial sap inoculation, transmission by thrips is not merely mechanical A minimum incubation period of 5 to 7 days in the insect is required The virus may be transmitted by both larvae and adults although adults cannot become infective by feeding on diseased plants The virus can be acquired from the plant only by the larval thrips, but it survives through metamorphosis, and the adults may become infectious without having fed as adults on a diseased plant The cause of this peculiar relationship is not known The life of the adult is considerably longer than the maximum incubation period of the virus in the insect's body, and so it cannot be explained on the basis of a long incubation period Inasmuch as the adults may transmit the virus acquired in the larvae stage, the size of the mouth parts constitutes no limiting factor in the movement of the virus particles The explanation of the inability of adult thrips to acquire the virus by feeding must await further knowledge of the physiology of the insect

After an individual insect has acquired the virus, it retains it for several weeks, although its transmission during this period is often erratic The virus is not transmitted congenitally through the eggs of thrips or the seeds of tomato The latent period of the virus in the tomato is 8 to 18 days, and its length is influenced by temperature and other factors, the average being approximately 12 days The virus, in extracted juices, is short-lived, losing its potency in 3 hours It is also sensitive to heat, being inactivated in 10 minutes at 42 degrees centigrade

Thrips are very small insects of the order Thysanoptera The adults are dark brown or black They live on a wide range of

host plants and are often destructive independently of virus transmission   They feed on the epidermis of leaves and other succulent tissues with a rasping and sucking action   Feeding wounds usually stand out as light-colored irregular spots on the leaf surface

Franklmiella lycopersici (Fig 164) reproduces both sexually and parthenogenetically   The minute colorless eggs are deposited beneath the epidermis near a vascular bundle   The eggs hatch in about twelve days   The larvae are light-colored and almost translucent   They feed on leaves immediately after
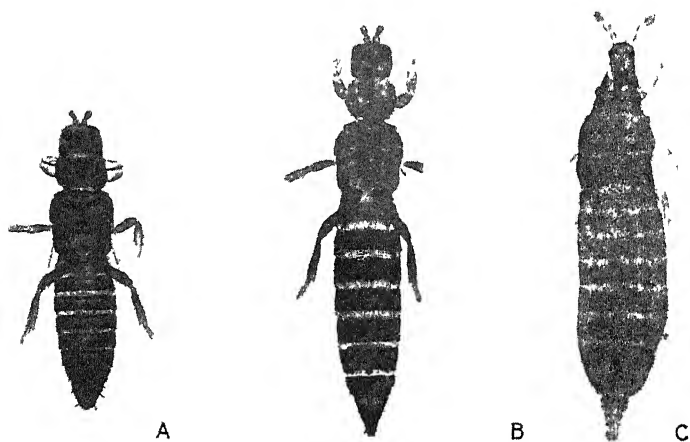
Fig 164 —*Franklmiella lycopersici*, one of the two vectors of the spotted wilt of tomato in Australia   A, adult male, B, adult female, C, full-grown larva Approx 45 ×   (*Photograph furnished by J G Bald*)

hatching   The larval period lasts from 6 to 17 days and includes two instars   A prepupal and pupal stage of 1 to 2 weeks is normally spent in the soil, after which the adult emerges, and the life cycle which requires a period of about 35 days is thus completed   The activity of the thrips is greatly increased by warm weather, Bald (1937) has shown a striking influence of the temperature on the number of plants becoming infected 12 days later

Yellow Spot of Pineapple (Ananas Virus 1) —Yellow spot is one of the major diseases of pineapples in the Hawaiian Islands It was first thoroughly defined and described by Illingworth in 1931, but the cause of the disease was not known definitely at

that time   The virus nature of the disease and its method of spread were determined definitely by Linford in 1932   The disease was first observed in a small area in Hawaii in 1926   In subsequent years, it spread rapidly throughout the islands   Yellow spot was reported in the Philippines in 1935 (Serrano 1935)

The first symptom of yellow spot is the so-called "initial spot," a small ($\frac{1}{8}$ to $\frac{1}{2}$ inch), slightly raised, yellowish spot on the upper surface of a leaf   It has a dark center surrounded by a
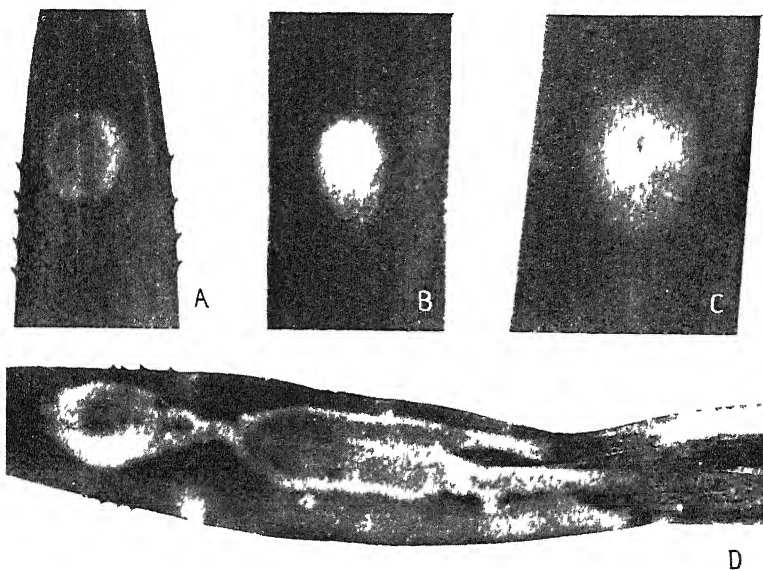
Fig   165 —Pineapple yellow spot   *A, B,* and *C,* "initial spots," or primary symptoms, *D,* more advanced symptoms involving a long chlorotic streak and a large area of necrosis at its base   The original initial spot is seen at the left near the apex of the leaf   (*After Linford*)

halo of yellow (Fig   165)   The spot is usually found 3 to 8 inches from the base of the leaf, its center often marking the oviposition puncture of the vector (*Thrips tabaci* Lind)   A yellow streak eventually appears, extending from the spot to the white tissue at the base of the leaf   The streak is often constricted into small circular areas, giving a beadlike appearance. As the disease advances, the streak becomes water-soaked and finally necrotic   Similar symptoms appear progressively on the upper whorls of leaves   The tissues of the stem on the affected
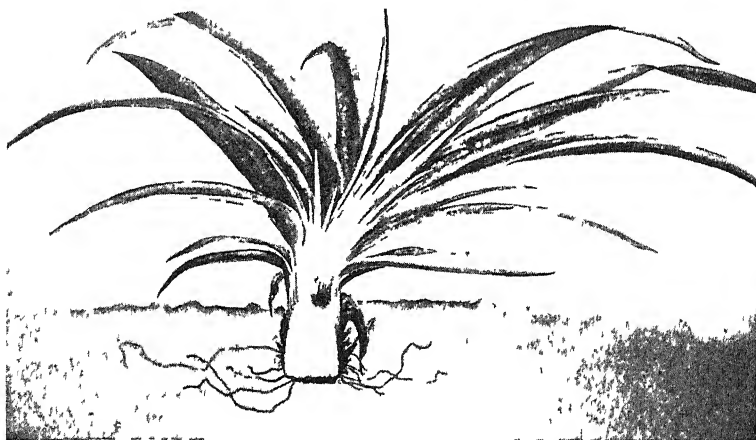
FIG 166 —Side rot, an advanced stage of yellow spot in which extensive necrotic areas have developed along one side of the plant   (*After Illingsworth*)
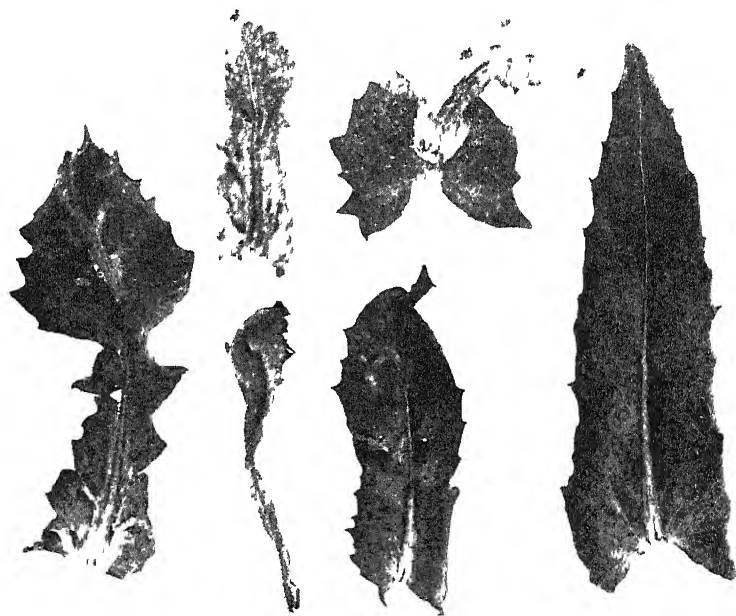
FIG 167 —Yellow spot of pineapple on leaves of *Emilia sagittata*, a common weed in the vicinity of pineapple fields in Hawaii   (*After Linford*)

side cease to elongate so that the axis becomes curved toward
the affected side   Finally, the entire plant droops and dies   The
distorted one-sided nature of the affected stems gave rise to the
earlier name "side rot" (Fig 166)

Several weeds growing in the vicinity of pineapple fields are
affected by the virus of yellow spot   Symptoms of various types
are produced on these weeds (Fig 167)   The most prevalent
weed host is *Emilia sagittata* (Vahl) DC , which is also a preferred
host of *T tabaci* Lind and has been shown to be the principal
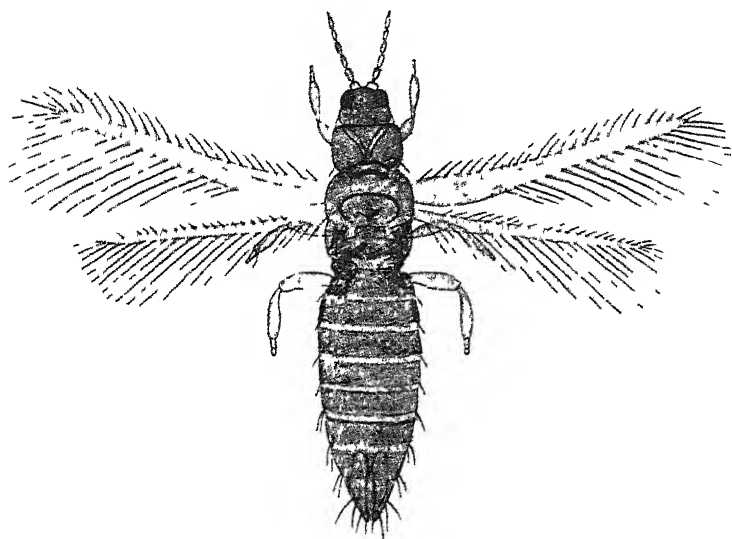
FIG 168 —*Thrips tabaci*, the vector of pineapple yellow spot   (*After Chittenden*)

source of infection on pineapples   Yellow spot has much in
common with spotted wilt of tomato and other plants, and it is
possible that the two diseases are caused by the same virus or
closely related viruses

Transmission of Yellow Spot—The disease is transmitted by
Thrips tabaci Lind (Fig 168), the only known vector   The
virus is not transmitted readily by artificial inoculation although
it can be transmitted in this way (Carter 1935)   An incubation
period of approximately ten days in the insect is required   As in
the case of spotted wilt, the vector is unable to acquire the virus
in the adult stage by feeding on infected plants   The virus is

acquired in the larval stage and survives pupation, the adults that develop from viruliferous larvae being also viruliferous The incubation period of the virus in pineapple and *Emilia sagittata* varies from 7 to 15 days

Thrips tabaci is an introduced species in Hawaii, but it is well distributed throughout the Hawaiian Islands   It has a wide host range, having been collected from 66 different species of plants of which *E sagittata* is one of the most important   Its life history has been studied by Sakimura (1932)

In Hawaii, *T tabaci* reproduces parthenogenetically throughout the year, and sexual reproduction is rare   There are two larval instars, a pupal and prepupal stage, that require approximately two weeks for completion   The eggs hatch in 4 to 5 days, and the average adult life is 32 4 days   The rate of development is slower in the cooler months, but the insect does not hibernate

Control of yellow spot by controlling the vector, although offering promise, has not been very effective   Biological control through imported parasites (*Thripoctenus russelli* Crawford and *T brui* Vuillet) has been attempted (Sakimura 1937), as well as control by dusting with nicotine (Carter 1932)

5 TRANSMISSION BY LACE BUGS, BIOLOGICAL AND SPECIFIC

Leaf Curl (Krauselkrankeit) of Sugar Beet (Beta Virus 3) — This is a destructive disease of sugar beets in local regions of Germany and Poland   It is similar in many respects to the curly-top disease of beets in America but apparently is not identical with it   For many years, the disease had been associated with infestations of the beet leaf bug (*Piesma quadrata* Fieb), but it was thought to be due to the toxic effect of the insect (Dyckerhoff 1927)   It is known now, however, that the disease is caused by a virus disseminated by *P quadrata*

The symptoms of leaf curl differ in several respects from those of curly top   Wille (1928) recognized primary symptoms that develop shortly after the insects feed upon the plant   These consist of light-colored spots marking the feeding punctures, a reduced turgor of the leaves, and occasionally premature death of the young plants   The secondary symptoms develop after a latent period that varies with numerous influencing factors They consist of a swelling and clearing of the veins, accompanied

by a distortion of the leaf   The petioles bend inward, forming a close compact "head-lettuce" type of growth   The plants are badly stunted, and the older leaves wither and die, forming a conical-shaped crown   The sugar content of the roots is greatly reduced, and the diseased plants often die prematurely

The host range has not been studied extensively, but it is known to include red beets, mangold, spinach, and *Rumex acetosa* (Wille 1929)   Wild-growing Chenopodiaceae as a rule

FIG 169 —Savoy of sugar beet   Note the curled and crinkled condition of the younger leaves   (*Photograph reproduced by courtesy of Division of Sugar Plant Investigations, U S Dept Agr*)

do not develop the secondary symptoms of the disease and, because they are all annual plants, are of no significance in overwintering the virus

Transmission of Leaf Curl—The lace bug (*Piesma quadrata* Fieb), is the only known vector of the disease   Leaf curl has been transmitted by artificial sap inoculation but in only a small percentage of trials   It is not transmitted through the seed of sugar beets   Nymphs of the vector are not capable of transmitting the disease, although adults bred from nymphs fed on

infected plants are virulifeious   The effectiveness of transmission and the severity of the symptoms caused depend to some extent on the number of insects and the time of feeding   Ten insects feeding for 2 hours are as effective as 3 insects feeding for 24 hours   One insect feeding for 24 hours or 10 insects feeding for 1 hour cause only mild symptoms   The virus is not transmitted congenitally in the eggs of the vector   The individuals of each new generation must acquire the virus by feeding on infected plants

The virus may overwinter either in infected plants or in the adult insects   The vector survives the winter as adults in a quiescent stage   They become active in the latter part of March or the first part of April   Egg laying begins in May, the eggs being deposited chiefly on the surface of the underside of the leaves   The first brood of adults appears in July   There are usually two broods a year in Germany   There are five larval instars   The control of the disease depends upon destroying the infected plants that might serve as sources of primary infec-

FIG 170 —
Piesma cinerea,
the vector of
savoy of sugar
beet   (*After*
Riley)

tion and upon control of the insect vector   The latter is accomplished with some success by destroying the cover along the drainage ditches in which the adults hibernate and by the use of trap rows of early planted beets on which the insects are killed by spraying

"Savoy" of Beets (Beta Virus 5) —"Savoy," a virus disease of sugar beets and garden beets, was reported in the United States in 1937 by Coons, Kotila, and Stewart   This disease is very similar to the *Krauselkrankheit* of Germany and is transmitted by *Piesma cinerea*   Coons, Kotila, and Stewart, however, state that it is distinctly different from both *Krauselkrankheit* and curly top

Affected plants have dwarfed, down-curled, savoyed leaves, and the symptoms are especially pronounced on the innermost leaves (Fig 169)   Primary symptoms are vein clearing and a thickening of the veinlets, giving a netted appearance to the dorsal leaf surface   In later stages, the roots are discolored, and the phloem is necrotic   The sugar content of affected roots is lowered

Piesma cinerea (Fig 170) is the only known vector   Viruliferous and nonviruliferous individuals are found   Savoy is not transmitted by *Myzus persicae, Aphis rumicis,* or *Eutettix tenellus*   The disease has not been transmitted by artificial sap inoculation   The latent period in the sugar beet is 3 to 4 weeks   The virus overwinters in affected beet plants and in the vector   The host range of the disease has not been determined   The economic importance of the disease is not great

6 TRANSMISSION BY WHITE FLIES, BIOLOGICAL AND SPECIFIC

Leaf Curl of Cotton (Gossypium Virus 1) —Leaf curl (leaf crinkle) is a destructive virus disease of cotton in the Sudan and in Nigeria   For many years, the disease was confused with injury caused by leaf hoppers, but in 1930 Golding, working in Nigeria, and Kirkpatrick, in Sudan, independently discovered the virus nature of the disease and demonstrated its transmission by a white fly (*Bemisia gossypiperda* Misra and Lamba)

The symptoms of leaf curl vary extensively   On some hosts and under some conditions, the leaves may show only a mosaic chlorosis or a downward curl of the leaf margins, but a definite crinkle produced by the "net-vein enations" is the most characteristic symptom on Sakel cotton   In all cases, the plants are stunted, and the yields are reduced

A similar disease of tobacco occurs in South Africa, Java, and Rhodesia   In Java, it is known as *kroepeck*   Storey (1931) and Thung (1932) have shown that kroepeck is transmitted by a species of *Bemisia*   Storey (1932*b*) concludes that kroepeck of tobacco is identical with leaf curl of cotton and is spread by the same vector (*B gossypiperda*)   Smith (1937*a*), however, lists these two viruses as being different

Transmission of Leaf Curl —The cotton white fly (*Bemisia gossypiperda*) is the only known vector of the disease (Kirkpatrick 1931)   Aphids and leaf hoppers have been tested but with negative results   The disease is not transmitted by artificial sap inoculation   All evidence indicates that the virus is not transmitted through the seed, and there is no evidence of transmission through the soil

The latent period of the disease in the cotton plant varies from 8 to 34 days but in the majority of cases is between 11 and 19

days   The vector may acquire the virus by feeding on an
infected plant 3 hours or less, and if an incubation period in the
insect is required it is not longer than 30 minutes   If the larvae
have fed on infected plants, the adults are viruliferous without
again feeding on infected plants   Viruliferous insects retain the
virus for their entire lifetime   The virus is not congenitally
transmitted through the eggs of the vector   The cotton white fly

Fig 171 —Cassava mosaic   A leaf showing typical symptoms of a severely
affected plant   (*After Storey and Nichols*)

was described as a new species by Misra and Lamba (1929), and
a few brief notes on its habits and life history were given

The virus of cotton leaf curl apparently survives the "dead"
season in the ratoon cotton which is nearly always infective when
new growth is made   Control of leaf curl will depend upon the
control of the white fly or the elimination of sources of primary
infection   Rotations planned with the view of eliminating the
ratoon cotton are being tried

Cassava Mosaic (Manihot Virus 1) —A mosaic disease of
cassava (*Manihot utilissima* Pohl) has been known in East Africa
since 1894 and is now known to occur throughout Western and

Central Africa where it incurs much loss   The disease is a typical mosaic disease although the symptoms vary widely   The leaves are mottled with distinct chlorotic areas and often are badly distorted (Fig 171)   Severely affected plants are stunted in proportion to the degree of leaf chlorosis   There are several strains of the virus, some producing much milder symptoms than others

Transmission of Cassava Mosaic —The virus of this disease apparently is not transmitted by artificial sap inoculation but is transmitted readily by grafting and by vegetative propagation It is not transmitted through the true seed   One or more species of white flies (*Bemisia spp*) are effective vectors of cassava mosaic   Insect transmission was first demonstrated by Ghesquiere (1932) and confirmed by Storey (1934) and Golding (1936) More complete studies of insect transmission have been reported by Storey and Nichols (1938)   There is some question of the identity of the vector   It has been referred to as a variety of *B gossipiperda* (var *mosaicivectura*) but one authority has identified specimens as a species closely related to *B nigeriensis* Corb (Golding 1936)   Perhaps more than one species may be involved

The vector is capable of transmitting the virus only by feeding on immature leaves, less than one-fourth their full length   A minimum latent period of the virus in the plant of 12 to 20 days is required   The incubation period of the virus in the insect vector is not known   Successful transmission experiments have all involved the use of large numbers of insects, and it is not known whether or not a single insect can transmit the virus

7 TRANSMISSION BY MITES

"Reversion" of Black Currants (Ribes Virus 1) —A disease of considerable economic importance affecting black currants in England and Western Europe is known as "reversion" (Fig 172)   The name was applied by growers and practical horticulturists because affected plants appear to revert to the wild type from which the improved cultivated varieties were derived   The symptoms are not clear-cut, and the disease has been confused with a number of other abnormal conditions   The most characteristic diagnostic symptoms are found on the leaves of the succulent vegetative shoots developing from buds formed the previous year near the top of the season's growth   The central

lobes of these leaves have a smaller number of submain veins and are more coarsely dentate than normal leaves   Reverted plants fruit very sparsely and eventually may become completely sterile (Amos and Hatton 1927)

Reversion has been studied most extensively in England where it is regarded as a major disease of black currants   The English

Fig 172 —Reversion of currants   The branch on the left is affected, the one on the right is normal   (*Photograph reproduced by permission of East Malling Research Station, Kent England*)

workers have presented strong evidence that the disease is caused by a virus   Because of the nature of the disease, its study has met with many difficulties, and it has not been easy to reach final conclusions in respect to many phases of the disease

Inasmuch as the symptoms of reversion resembled genetic mutations associated with chromosome abnormalities, Darlington

(1927) made a study of the chromosome complements in somatic cells from normal and reverted plants   The chromosome conditions in both plants were found to be essentially the same, and it was concluded that the possibility of a genetic explanation of the cause of reversion was remote

Transmission of Reversion —Reversion as it occurs in nature is closely associated with a condition known as "big bud" caused by the mite (*Eriophyes ribis*)   These mites live in the buds, inhibiting their normal expansion and causing them to swell   The buds are eventually killed, and the mites then migrate to new buds which they infest (Massee 1927)   Evidence has been presented (Amos, Hatton, Knight, and Massee 1927) to show that this mite is also the vector of reversion   Lees (1925) on
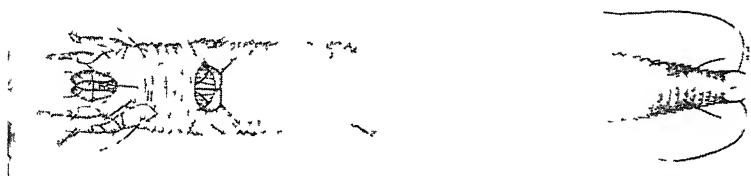
Fig 173 —*Eriophyes ribes*, the vector of reversion of currants   Very highly magnified   (*Drawing reproduced by courtesy of East Malling Research Station, Kent, England*)

the other hand, although recognizing the possibility of mite transmission, maintains that it can be transmitted in nature independently of the presence of the mite   Big bud is not believed to be a symptom of reversion, the two conditions are thought to be distinctly different   Big bud may occur on bushes that show no symptoms of reversion, and the disease is occasionally found on bushes that are free of big bud   In experiments in which buds were artificially infested with mites from reverted plants, 90 per cent of the successfully infested plants developed reversion and 92 per cent of the control plants not infested with mites remained healthy   Because of certain difficulties in working with the mites, the results are not conclusive beyond question, but there is strong circumstantial evidence supporting the view that reversion is transmitted by the mites   If this conclusion is proved to be correct, this is the first and only virus disease of plants known to be transmitted by a mite

The disease is definitely infectious and is transmitted by grafting but has not been transmitted by artificial sap inoculation However, the appearance of reversion on a number of stocks, grafted with reverted scions that did not make a successful union, led Lees (1925) to conclude that the virus was transmitted by contact   The disease is not transmitted by the seed   The incomplete and often contradictory nature of much of the data dealing with the transmission of this disease makes it difficult to reach a satisfactory conclusion concerning its nature and methods of transmission

The natural spread of the disease in the field has been studied by Amos and Hatton (1928), who showed that a rapid spread could be traced to a center of exceptionally heavy infestation of the big-bud mite and reversion   Careful roguing and the selection of healthy plants for cuttings give promise of successful control of the disease

Eriophyes ribis, the black-currant-gall mite, is a very small mite with a relatively long cylindrical body (Fig 173)   The females measure only 220 microns in length, and the males are about 150 microns long   They feed upon several species of *Ribes* but appear to be confined to plants of that genus   The mites leave the old buds in late spring, and in the latter part of May they enter the new buds and make their way to the center where they breed   Eggs may be found in the buds the year round and are deposited, also, on the leaves and in the blossoms   They hatch within 3 to 7 days   Infested buds begin to swell in late summer, and the following spring they fail to open and usually die   The mites are disseminated from bush to bush by insects and by wind

8 NATURE OF TRANSMISSION OBSCURE

Wheat Mosaic (Triticum Viruses 1 to 7) —In 1919, a destructive disease of winter wheat was observed in Illinois and Indiana (McKinney 1923, 1937)   The true nature of the disease was not recognized at that time, but further investigations have shown the condition to be a complex one caused by several closely related viruses (McKinney 1937)   One or more of the viruses have been reported from Illinois, Indiana, Kansas, Nebraska, Maryland, North Carolina, and Virginia   The viruses affect certain varieties of wheat, barley, rye, emmer,

spelt, and einkorn They are most destructive on certain varieties of winter wheat Spring wheat is rarely affected although it is susceptible if planted in the autumn in a region of mild winters The diseases have not caused a great economic loss partly because of their limited distribution and partly because of the availability of suitable resistant varieties of winter wheat However, they are potentially very destructive because entire fields may be made worthless in regions where the diseases are prevalent

The symptoms caused by the viruses vary greatly with the strain or strains involved, the variety of suscept, and environmental conditions One of the principal effects is a dwarfing that results in a rosette type of growth that does not head out Various degrees of chlorosis in a variety of patterns are often observed, but chlorosis is not universally present on affected plants

Transmission of Wheat Mosaic —The viruses of wheat mosaic are transmitted readily by artificial sap inoculation, but the methods of transmission in nature are not definitely known These viruses are unique in that they appear to be transmitted in nature only through the soil (Webb 1927, 1928) Although it is possible that aphids may transmit at least one of the viruses (Haskell and Wood 1923), insects that feed upon the aerial parts of the plant apparently are not important in natural transmission The viruses are not transmitted through the seed, but the disease develops in severe form when seed are planted in infested soil in insectproof cages Plants grown in sterilized soil or in noninfested soil do not become diseased although they are not protected from insects The viruses may survive indefinitely in the soil and cannot be removed by extensively washing the soil Infection takes place through the roots and through the crown of the plant, but the mechanism of ingression is not known This aspect of the problem needs further study

Latent (*X*) **Virus of Potato** (**Solanum Virus 1**) —This unique virus was discovered by Johnson (1925), who inoculated tobacco plants with juice of potato plants that appeared to be free of virus infection and found that distinct virus symptoms were produced on the inoculated tobacco plants Further experiments showed that practically all the commercially grown American varieties and many European varieties, however,

develop characteristic symptoms when inoculated with the virus   Several other species of solanaceous plant also are susceptible to the virus

Transmission of the X Virus —Although this virus is readily transmitted by artificial sap inoculation, it is not transmitted by aphids or other common insect vectors, nor is it transmitted through the true seeds of potatoes   Its widespread occurrence in nature, however, indicates that it must spread rapidly, but the method of transmission is still unknown   The universal occurrence of this virus in the older American potato varieties may be explained in part by the fact that the virus produces no injury to the plants and is perpetuated through the tubers   If the virus causes no injury that decreases the ability of infected plants to compete with healthy ones, it would be expected that, in time, the vegetative progeny would soon approach the condition of universal infection

Smith (1937) has suggested that this virus may be transmitted by a flower-feeding species of thrips, but there is no record of the possibility having been thoroughly investigated   Loughnane and Murphy (1938) have presented evidence to show that the virus may be transmitted from plant to plant by leaf contact when subjected to the action of an oscillating electric fan   These authors are of the opinion that the virus spreads in nature by leaf contact, aided by the action of the wind   Cockerham (1937) found no correlation between the flowering habit of the potato varieties grown in Scotland and the presence of the *X* virus   It was observed, however, that the varieties found to be free of the *X* virus were those which reacted by severe lethal necrosis when inoculated with it   Infected individuals of these varieties would be eliminated, only the virus-free plants surviving   Thus the virus is said to be self-eliminating in those varieties which react in this way to it

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CHAPTER X

INSECTS AND PHYTOPATHOGENIC PROTOZOA

Protozoa are single-celled animals without true organs and tissues There are innumerable species, of widely varying size, morphology, and life habits Many species are harmless or even beneficial, but some have been recognized for many years as the cause of fatal or severe diseases of man and other animals Such devastating diseases as malaria, sleeping sickness, and dysentery are caused by protozoa Insects or other arthropods have proved to be the principal vectors of a relatively large percentage of the protozoa that are pathogenic to animals, and the suppression of epidemics of these diseases has hinged largely upon the control of the arthropod vector Plants, on the other hand, are comparatively free of protozoal diseases In fact, it has been known for only a relatively short time that there are protozoa parasitic on plants

Protozoa in Laticiferous Plants —In 1909, Lafont discovered a flagellate inhabiting the latex of three species of *Euphorbia* He described and named the organism *Leptomonas davidi* This discovery created much interest among protozoologists and those concerned with human and animal diseases caused by flagellates In the next few years, the same or similar species were reported from a large number of laticiferous plants in various parts of the world, mostly in tropical or semitropical regions (Franca 1911–1922, Franchini 1922–1923, Migone 1916, and others) By 1925, flagellates had been reported in more than 50 species in six or more families of laticiferous plants Partly because few students of plant pathology were trained in protozoology and partly because of the lack of economic importance of the plant-parasitic protozoa, these organisms have received very little attention from plant pathologists Brief reviews of the literature dealing with endophytic protozoa appeared in *Zeitschrift fur Pflanzenkrankheiten* (Nieschulz 1922) and in *Phytopathology* in 1925 (Bensaude)

The protozoa found in the latex of plants are, for the most part, free-swimming flagellates. They are usually pleomorphic, the typical form being approximately 15 to 20 microns in length (Fig 174). Multiplication, as most frequently observed, is by longitudinal binary cleavage. The protozoa are not easily cultivated on artificial media although certain species have been cultured successfully. Nearly all species found in plants have been found also in the intestinal tract of some plant-feeding Hemipterous insect. There are many similar species that have been found only in the intestinal tracts of insects. It has been suggested that probably all the endophytic protozoa were originally members of the intestinal fauna of insects and that they have adapted themselves to life in the plants on which the insects feed. Such progressive adaptation appears to be a char-
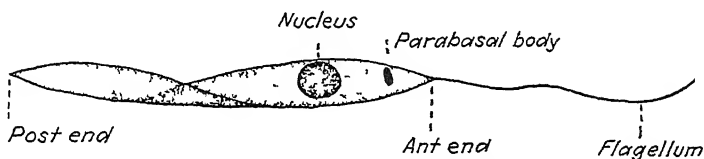
FIG 174 —A flagellate from the latex cells of milkweed   (*After Holmes*)

acteristic of this group of protozoa. Referring to the order Protomastigida, which includes these flagellates, Calkins (1933) states that they "well illustrate the power of continued adaptation to new conditions in the host, leading to progressive parasitism whereby an original commensal may become a lethal parasite"

There has been some question as to the pathogenicity of the protozoa found in laticiferous plants. Lafont (1909) and Franca (1920) claimed that *L davidi* Lafont caused a real disease of affected euphorbias. They state that infected plants may be recognized easily by a generally starved appearance followed by a yellowing and final wilting of the leaves. Infection is often localized in a single branch, which is stunted and much shorter than the normal ones. Strong (1924) also has reported striking symptoms of infection on species of *Euphorbia*, and more recently Sassuschin (1933) made similar claims for the flagellates (*L davidi*) on *E uralense* in southeastern Russia. On the other hand, Bouet and Rouband (1911), Rodhain and Bequaert (1911),

and Noe and Stévenel (1911) have maintained that it is difficult or impossible to distinguish infected from noninfected plants

Migone (1916) described a flagellate from milkweed (*Araujia angustifolia*) in Paraguay and named it *L elmassiani*   All the plants growing in one region were uniformly infected and showed no signs of injury   Four years later Franca (1921) described a new species of protozoa (*L bordasi*), isolated by Migone from a different milkweed (*Morrenia odorata*), and in this case also no injury was evident   Holmes (1925a) likewise concluded that *Herpetomonas* (*Leptomonas*) *elmassiani* (Migone)[1] in milkweed (*Asclepias syriaca* L) in North America was not pathogenic It is entirely possible that these contrasting opinions are, to some extent, caused by differences in environmental factors in different localities, but in any case, it is evident that the flagellates in laticiferous plants in general cause very little injury and are not of great economic importance   However, the phenomenon is of general biological interest from several viewpoints

The relative lack of virulence of the flagellates in laticiferous plants can be explained in part by the nature of the latex ducts that they inhabit   There are two distinctly different types of laticiferous duct, latex vessels and latex cells (Fig 175)   Both types consist of single living cells containing many nuclei and extensive vacuoles in which the latex is found   The latex is secreted by the cytoplasm and accumulates in the vacuoles   A latex vessel arises by the dissolution of the end walls of a row of meristematic cells to form a long multinucleate vessel   A latex cell results from the elongation of a single cell, which may

[1] There has been some confusion in the use of the generic names applied to the endophytic protozoa   Lafont used the name *Leptomonas* because the flagellates he observed in the latex of plants agreed morphologically with the genus *Leptomonas* Kent, all the previously known species of which were confined to the bodies of invertebrate animals   Holmes (1925b) has used the generic name *Herpetomonas* because "the genera *Leptomonas* and *Herpetomonas* were united in 1884 by Butschli, the first reviser, under the name of *Herpetomonas*"   Some authorities on protozoology (Wenyon 1926), however, continue to recognize both of these genera but place the plant-inhabiting flagellates in a third genus *Phytomonas*, created by Donovan in 1909   The genus *Phytomonas* Donovan is defined by Wenyon (1926) as "flagellates which resemble those of the genus *Leptomonas*, but differ in having both an invertebrate and a plant host "   Further confusion has been caused by the use of the name *Phytomonas* for a genus of phytopathogenic bacteria (Bergey *et al* 1923)

grow and branch like a fungus mycelium   Latex vessels may
unite to form an extensive anastomosing system, but latex
cells occur as independent units   Most of the species of Euphor-
biaceae and Asclepiadaceae have latex cells rather than latex
vessels   Apparently the flagellates are confined to the latex
cells and are unable to penetrate the cell walls or to parasitize
the other plant tissues   Not only are they confined to the latex
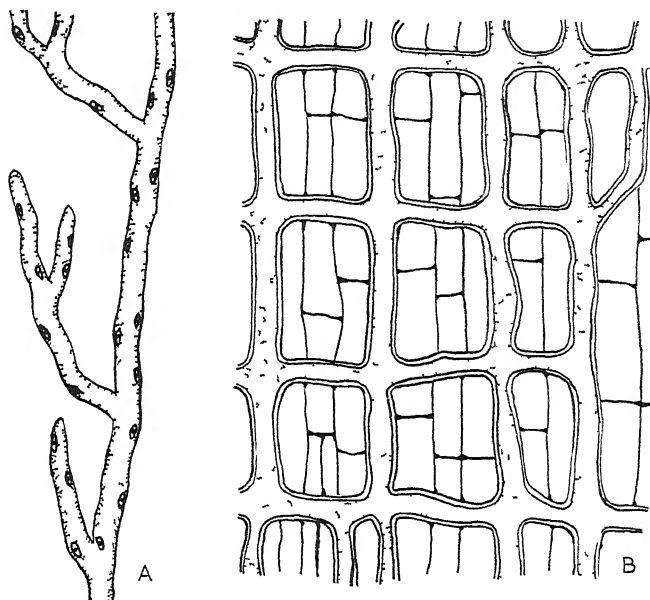
FIG 175 —Diagrammatic representation of two types of latex duct   *A*   a
latex cell (each cell is multinucleate, and although it may ramify extensively
it is a single cell), *B*, a latex vessel formed by the anastomosing of a number of
individual cells   Some laticiferous plants have latex cells, and others have latex
vessels   Endophytic protozoa have been found chiefly in latex cells   (*After
Holmes*)

cells but they occur only in the vacuoles   The latex cells are
limited in extent, and each cell, although it may be extensively
ramified, is usually independent of the others   For this reason,
the flagellates are localized so that they do not cause a systemic
infection of the vital tissues   A systemic infection of the vas-
cular elements would be likely to be much more injurious to the
plants

When the protozoa were first discovered in plants, it was
observed that they were very similar in morphology to flagellates

previously found in the intestinal tracts of numerous insects, a fact which suggested that they were insect-transmitted   Lafont (1911) experimentally transmitted the flagellate (*L davidi*) to plants by means of *Nysius euphorbiae* Horvarth, a Hemipterous insect that feeds exclusively on Euphorbiae   Bouet and Rou-
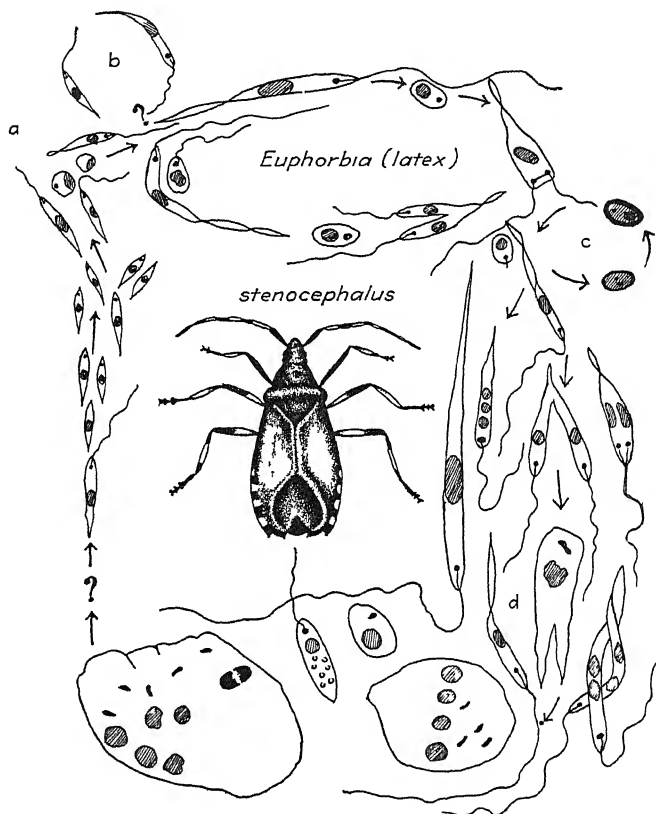
Fig 176 —The life cycle of *Leptomonas davidi* and its vector (*Stenocephalus agilis*), according to Franca   *a*, infective forms, *b* forms found in the fruits of Euphorbia, *c*, encysted forms in feces of the insect, *d*, forms found in the intestinal tract of the insect   (*After Franca*)

band (1911) transmitted the flagellate to plants with *Dieuches humilis* Reut , another Hemipterous insect   Franca (1920) showed that *Stenocephalus agilis* (Fig 176) was the chief vector of *L davidi* in Portugal

Franca (1920) was able to transmit the flagellates from plant to plant with *S agilis* as found naturally infected in nature

He observed flagellates in the intestinal tracts of the insects feeding on infected plants, whereas those feeding on noninfected plants were free from protozoa By means of feeding experiments, he was able to show that the flagellates found in the insect were identical with those in the latex of infected plants He studied also the complete life cycle of the organism as it occurred in both insect and plant hosts, describing what he interpreted as a true cyclic development comparable with that of certain insect-transmitted protozoa parasites of animals Insects obtained from noninfected plants were fed on infected plants, and at frequent intervals specimens of the insect were killed and examined During the first 3 days, the flagellates found in the intestinal canal of the insect were in active division and were very similar to the forms observed in the plant tissues After the third day, multinucleated forms were observed, and these were interpreted as having been formed by isogamic conjugation After 8 days, very small forms were found throughout the intestinal tract and in the salivary glands These were often without a flagellum and varied in size from 4 5 to 7 microns long by 0 8 to 1 5 microns wide, whereas the forms found in plants are from 16 to 20 microns long and 1 5 to 2 microns wide The small "metacyclic" forms are considered by Franca as the infective stage in the life cycle The complete life cycle of *L davidi*, as interpreted by Franca, is illustrated in Fig 176 This is the most complete study that has been reported on the association of the endophytic protozoa with insect vectors The evidence presented by Franca of a true cyclic development in the insect vector is in need of further study Considering the numerous reports of endophytic protozoa in many parts of the world, it is unfortunate that more intensive studies of methods of transmission in different localities have not been made Many of the known insect vectors are active only at night, and it is possible the nocturnal habits of vectors may explain why they have been overlooked in so many cases

Strong (1924) has described a flagellate (probably *L davidi*) found in Euphorbia in Central America He showed that it was transmitted by *Chariesterus cuspidatus*, a coreid bug, and demonstrated it in all parts of the intestine and in the salivary glands of the vector The organism manifested a greater diversity of form in the insect than in the latex of the plants

Forms with the posterior and twisted in a helicoid manner, small round or oval forms, with or without a flagellum, and typical cystic forms were observed   Slender, short forms with a rigid flagellum were the most common ones in the salivary glands Reproduction through binary fission was demonstrated in the insect, but no multiple fission was observed

Holmes (1924, 1925*a*, *b*, *c*) found *Oncopeltus fasciatus* (Dall), a red-and-black Hemipterous insect, closely associated with milkweeds infected with *Herpetomonas elmassiani* (Migone) and considered it as the most probable vector   The geographical distribution of the insect vector coincided very closely with the distribution of infected milkweeds (Holmes 1925*b*)   Both adults and nymphs contained flagellates in their salivary glands, but the flagellates were not observed in the intestinal tracts of any of the specimens examined   These flagellates were similar to ones found in the plants in all respects except size   Those found in the insects were somewhat larger than those in the plants, but the smaller individuals found in the insects were well within the range of those in the plants   A characteristic twist of the body was present in flagellates from both sources   It was concluded, therefore, that the same species was involved in both cases No cyclic changes of the protozoa in the insect body were reported

The salivary gland of *O fasciatus* is a three-lobed gland located in the thorax and emptying through a single efferent duct   The flagellates were very abundant in the most dorsal lobe, and a few were found in the anterior lobe, but the posterior lobe was always free of them   It is not known how the salivary gland becomes infected, for the protozoa were found neither in the alimentary canal nor in the blood cavity

DuPorte (1924, 1925) reported the presence of protozoa in the latex of the following plants   *Asclepias syriaca, Convolvulus sepium, Norus alba, Lactuca canadensis, L sativa, Apocynum sp , Hieracium aurantiacum, Taraxacum officinale, Ficus sp , Sonchus spp , Euphorbia sp ,* and *Chelidonium majus*   No descriptions were given, although both flagellates and amoeba were mentioned No insect vectors were reported   In two cases, *A syriaca* and *C sepium*, it was stated that the protozoa were transmitted through the seed of infected plants

Noguchi and Tilden (1926) have reported comparative studies of flagellates from insects and plants   These authors described

and named two species from bugs feeding on laticiferous plants and from the plants as follows *Herpetomonas oncopelti* from *Oncopeltus fasciatus* (probably the same as the one described by Holmes from the same insect as *H elmassiani* Migone), and *H lygaeorum* from *Lygaeus kalmii,* a bug closely related to *Oncopeltus* These authors compared these flagellates and others obtained from latex of plants and from other insects with the Leishmania forms that are parasitic on higher animals and found them to be quite different

Franchini (1922*d*) has described a flagellate infection of cabbage, a nonlaticiferous plant   The plants were infested with pentatomid bugs (*Pentatoma ornatum* and *P oleraceum*), and the affected leaves were yellow and wilted   Smears made from the leaves and the intestines of the insect revealed the presence of similar flagellates   However, the evidence that the protozoa were true parasites within the tissues of the cabbage is not convincing   Franchini (1923*d*) claims to have inoculated *Euphorbia* plants successfully with flagellates from the intestines of several species of fly, but the methods of infection in nature and the life cycles of the protozoa were not determined   However, latex was recognized in the intestinal tracts of flies and it was suggested that the feces of flies feeding on droplets of latex secreted by the corolla of the flowers might account for natural infection   Many of the reports of Franchini have been fragmentary, containing very little experimental evidence, and later work supporting his conclusions has not been reported

Some studies have been made to determine if the plant-inhabiting flagellates are capable of infecting vertebrates Strong (1924) has shown that in Central America a bug, [*Charresterus cuspidatus* (Distant)] transmits the flagellates of *Euphorbia* and that the bugs are eaten by a lizard (*Cuemidophorus lemiscatus*)   In the posterior portion of the intestines of the lizard a flagellate indistinguishable from the insect flagellate was found   These were inoculated into monkeys, dogs, guinea pigs, and mice, but only one lesion was obtained, on the monkey, in which flagellates of the Leishmania type were present   The ulcer and the flagellates resembled somewhat the lesions of a cutaneous leishmaniasis prevalent in the locality   The evidence, however, is not sufficient to justify the conclusion that the endophytic protozoa are the cause of the disease affecting man

Phloem Necrosis of Coffee—Even though the flagellates found in laticiferous plants are not highly pathogenic, protozoa cannot be ignored as plant pathogens. Stahel (1931, 1932, 1933, 1934) has shown that the destructive phloem necrosis of the coffee tree in Dutch Guiana (Surinam) is caused by a flagellate which he named *Phytomonas leptovasorum*. According to

FIG 177 —A coffee tree affected with phloem necrosis   (*After Stahel*)

Stahel, phloem necrosis is the most destructive disease of coffee in Surinam. The disease has been known for more than 30 years, but its nature and cause were not understood. It occurs in two forms, one acute and the other chronic, but all intergrading types may be found. The chronic form is the most common and is characterized by a premature yellowing and dropping of the leaves. New leaves are put out, but they are smaller and fewer than the first ones. Finally, after a period varying from

3 to 12 months, the entire tree dies (Fig 177) In the acute form the leaves turn yellow and within 1 or 2 days begin to wilt, and the entire tree will usually die within 1 to 2 months This type is most frequent in the beginning of a dry period but may occur at other times

As the name of the disease implies, the seat of the trouble is in the phloem tissues which become necrotic while the adjacent vascular tissue is discolored by impregnation with wound gum Preceding the appearance of necrosis, many of the sieve tubes undergo multiple division, a condition giving rise to many abnormally small sieve tubes The necrotic sieve tubes always contain large numbers of flagellates resembling in many respects those found in the latex of euphorbias and other laticiferous plants (Fig 178) Although microscopic examination of living material and stained preparations leave no doubt as to the protozoal nature of the pathogenic organisms, Stahel has not been able to culture them in artificial media

The method of transmission of phloem necrosis is not definitely known, but much circumstantial evidence indicates that an insect vector is responsible In 1935, Bunzli, who made an extensive study of insects associated with the roots of the coffee plant, concluded that a coccid (*Rhizoecus coffeae*) was the vector This insect, which is attended by the ant (*Rhizomyra paramaribensis*), feeds upon the roots of the coffee tree, and in a limited number of uncontrolled experiments Bunzli obtained data which led him to believe that it was the agent of transmission Stahel, however, was unable to confirm Bunzli's results and concluded that the bug (*Lincus spathuliger* Bredd[1]) is the true vector, although definite proof of transmission was not obtained

The improbability of *R coffeae* serving as a vector is indicated by the fact that the salivary canal of its mouth parts is too small to permit the flagellates to pass, being only $\frac{1}{4}$ micron in diameter, whereas the flagellates are 1 to $1\frac{1}{2}$ microns thick *Lincus spathuliger*, however, has a salivary canal measuring 4 microns in diameter This Hemipterous insect is also attended by ants (*Pheidole biconstricta*), feeds on the tap root near the surface of the ground, and is potentially an effective vector

[1] Originally referred to as *L securiger* but corrected by correspondence with the author

In view of the fact that the flagellates of laticiferous plants are transmitted by Hemipterous insects, it seems only reasonable to suspect that similar insects may be responsible for the transmission of *P leptovasorum* It would be difficult to account for their transmission by any other agency than insects It is
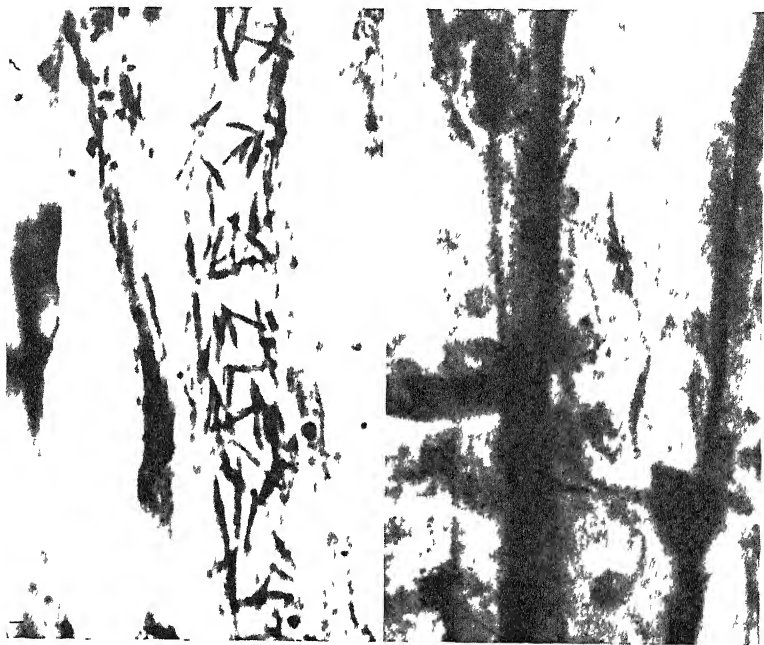
FIG 178 —*Phytomonas leptovasorum*, the flagellate pathogen of phloem necrosis of coffee, in the sieve tubes of affected coffee plants   (*After Stahl*)

hoped that further investigations will soon clear up this important phase of the problem

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CHAPTER XI

MITES, NEMATODES, AND OTHER SMALL ANIMALS AS VECTORS OF PLANT DISEASES

In previous chapters, our discussion of vectors of plant diseases has been limited almost entirely to insects However, there are, in addition to insects, a number of small animals that serve as effective vectors Among these may be mentioned mites, nematodes, slugs, earthworms, and birds A few examples of disease transmission by these animal vectors will be discussed briefly

MITES

Mites are small, insectlike arthropods closely related to spiders and ticks They belong to the order Acarina, which includes both mites and ticks The principal difference between mites and ticks is one of size, the larger members of the order being known as ticks, the small ones as mites The latter differ from insects in having typically four pairs of legs, no antennae, no true jaws or compound eyes, and no distinct body segmentations (Fig 179) One family (Eriophyidae), however, is characterized by having only two pairs of legs (Fig 173) The larvae of most species, immediately upon hatching, have only three pairs of legs, but they soon molt and transform into nymphs having all four pairs After one or two additional molts, they acquire external sexual organs and assume the adult form Mites are found in many localities and have a wide variety of habits Some are free-living, but many are parasitic upon animals or plants, causing much economic loss Only a few species of mite have been incriminated definitely as vectors of plant diseases, but they have not been studied extensively from this viewpoint

An excellent review of the Acarina is given by Banks (1915), who recognizes 8 superfamilies composed of 31 families Those mites most closely associated with plants and plant diseases are found chiefly in the families Eriophyidae and Tyroglyphidae *Pediculopsis graminum* Reut , the vector of *Sporotrichum poae,*

causing silver top of June grass and bud rot of carnations, belongs to the family Tarsonemidae, many of which feed on growing plants and cause various deformities

The Eriophyidae are among the smallest of mites, few of them reaching more than 250 microns in length, many are only half as long   The body is usually much elongated with a multiannulated abdomen   The adult characteristically has two pairs of legs All species of the Eriophyidae feed on plants and usually cause galls   The forms of the galls vary, but, in general, they are characterized by the production of a velvety mass of abnormal
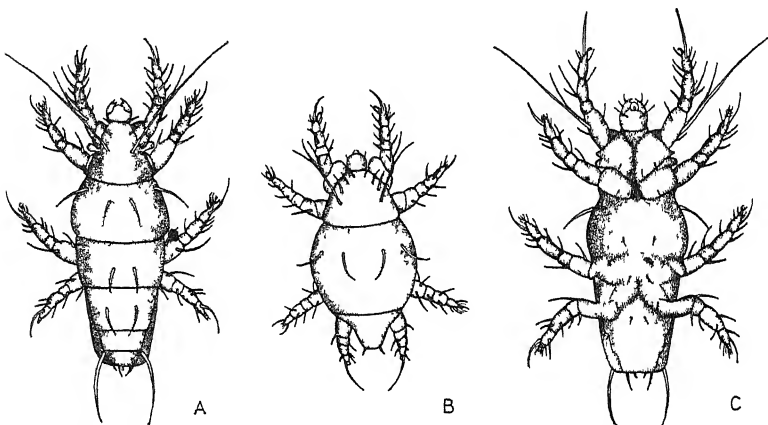
Fig 179 —*Pediculopsis graminum* Reut   The mite that serves as a vector of bud rot of carnations   *A*, male dorsal view, *B*, male ventral view, *C*, nongravid female, dorsal view   (*Redrawn after Stewart and Hodgkiss*)

trichomes, either exposed on the surface or enclosed in pouches or capsules formed by the leaf tissue   The term "erinose" is applied to the galls produced by these mites

Some species inhabit buds, causing them to become abnormally large but inhibiting normal opening and growth   *Eriophyes ribis* causes big bud of currants in England and Europe, and is the best known of the bud-infesting species   It also is a vector of "reversion," a virus disease of currants

The Tyroglyphidae are most frequently associated with stored foods and decaying plant tissues   A few species have been incriminated as vectors of plant pathogens, and several others have been under suspicion   The family is characterized by the occurrence of a peculiar and unusual nymphal stage, the so-called

"hypopus," which is strikingly different from the other stages
The body of the hypopus is hard and tough it has no mouth, and
its legs are short and ill-adapted to walking For many years it
was not recognized as a stage of development but was considered
a distinct species It is now known to be a stage especially
adapted for ensuring distribution to new sources of food The
hypopus has, on its ventral surface, a number of suctorial disks
by means of which it attaches itself to an insect (Fig 181) Hav-
ing no mouth parts, it does not feed upon the insect but merely
uses it as a means of transportation After transportation to a
suitable locality, its hold on the insect is released, and the mite
undergoes metamorphosis into a typical nymph and begins to feed
again Tyroglyphid mites that inhabit the bark of trees are
transported by bark beetles and other bark-infesting insects
Those which live on decaying material are transported by flies
and other insects that are attracted to decayed plant tissues
The British Tyroglyphidae were studied extensively by Micheal
(1901, 1903), and a revision of the family was published by Banks
(1906)

**The Relation of Mites to the Silver Top of June Grass and
Bud Rot of Carnations** —Silver top of June grass (*Poa pratensis*
L) and other grasses is a disease that causes the flower panicles
to wither before they have become fully expanded The affected
parts lose their chlorophyll and become bleached and silvery in
color, suggesting the name "silver top " For many years, the
trouble was thought to be caused by insects, but in 1908 Stewart
and Hodgkiss reported evidence from work begun in 1902 which
showed that the condition was caused by a fungus disseminated
and inoculated by a mite The fungus was described and named
Sporotrichum poae by Peck in 1903 The mite was identified as
Pediculopsis graminum Reut , which had previously been reported
by Reuter (1900) as associated with the disease in Finland The
mites (Fig 179) crawl down the grass culms under the sheath to
the base of the panicle where the tissues are relatively soft and
succulent They inoculate the tissues with the fungus which
they carry with them The mites apparently feed on the fungus
and the decayed tissue that develops at the base of the panicle

Carnation bud rot is a disease characterized by an internal
decay of the unopened buds resulting in the failure of the buds to
expand into normal flowers (Fig 180) On dissecting the

unopened buds the interiors are found in various stages of decay,
and numerous mites always are present in the decayed tissues
Bud rot of carnations was first described in Nebraska by Wolcott
in 1905   He attributed the injury entirely to mites   The follow-
ing year, Heald (1906) reported the same trouble to be caused by
a fungus transmitted by mites   The fungus at first was thought
to be a species of *Fusarium* but was later identified as a species of
Sporotrichum   A more complete description of the trouble was
published by Heald (1908) with experimental proof of the patho-
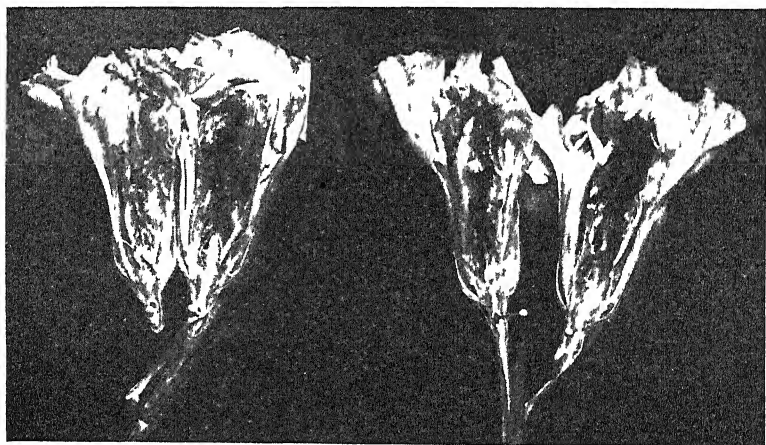
FIG 180 —Two carnation flowers cut open to show the internal decay asso-
ciated with infestation by the mite *Pediculopsis graminum*   (*Courtesy of the
New York Agricultural Experiment Station, Geneva*)

genicity of the fungus and its transmission by mites   The fungus
was described and named *S anthophilum* by Peck   The mite
was described and named *Pediculoides dianthophilus* by Wolcott
(1908)   Later in the same year, Stewart and Hodgkiss (1908)
published a report of their study of the same disease in New
York   These authors concluded that bud rot of carnations and
silver top of June grass were caused by the same fungus (*S poae*
Peck) and that the mite was the same as that described in 1900
by Reuter as *Pediculopsis graminum*

The evidence obtained by all workers on this disease indicates
that the fungus is entirely dependent upon the mites for its intro-
duction into the carnation buds   Whether or not the mites are
dependent upon the fungus in any way has not been determined,

but the decayed tissue appears to be favorable for their development. The method of overwintering of the fungus is not known. There is no evidence to show whether the fungus is constantly associated with the mites or whether the mites become contaminated from some other source each year. The eggs are not deposited by the female mites, the young developing to maturity inside the bodies of the gravid females, which on death disintegrate to liberate numerous fully developed young. The mites probably survive the winter as adults in protected places.

As described by Heald and by Stewart and Hodgkiss, carnation bud rot was confined entirely to greenhouse carnations, but recently Reiter (1935) has reported severe outbreaks of the disease in field-grown carnations. The carnations had been planted in soil that had been in June-grass sod the previous year, and the association of the mites with the decayed buds in the field was in all respects similar to that found in greenhouses.

Mites as Vectors of the Blue-stain Fungi—Leach, Orr, and Christensen (1934) called attention to the possible role of mites in distributing the spores of the blue-stain fungi in Norway-pine logs. It was observed that from 1 to 12 or more small mites were attached to the ventral part of the thorax or in the concave wing declivities of nearly all the bark beetles (*Ips pini* and *Ips grandicollis*) found in logs infested with blue stain. The mites (which were not identified) had obviously attached themselves to the beetles before they had emerged from the infested logs. Careful examination of the logs showed mites running about in nearly all freshly made tunnels. They were also abundant in old tunnels. These mites, which apparently belong to the Tyroglyphidae leave the beetles when they enter a log and feed on the fungi and decomposing bark tissue. When the beetles of the new brood are ready to emerge, some of the mites attach themselves to the beetles and are thus carried to new trees or logs. Microscopic examination of the mites taken from the beetles, as well as cultures made from the mites, showed that spores of the blue-staining fungi were often disseminated by them.

The possibility of the Tyroglyphid mites serving as vectors of the Dutch elm disease has been recognized by Jacot (1934, 1936). He found three species common in the bark of elms affected with the disease. They were usually associated with the brood tunnels of elm bark beetles (*Hylurgopinus rufipes* Eich. and *Scolytus*

multistriatus Marsh) or with those of the flat-head borer (*Saperda tridentata* Oliv)   The mites were identified as follows *Moniczciella arborea* Jac , *Histiogaster fungivorax* Jac , and *Megninietta ulmi* Jac

The migration of these mites from tree to tree is effected chiefly through the hypopial nymph, which is more drought-resistant than the normal form and which attaches itself to any passing insect and is transported by the insect to a new location   The hypopial nymphs are incapable of feeding and do not carry spores internally but are capable of disseminating those adhering to bristles, legs, or body plates   Many of the mites were taken in bark-beetle tunnels which bore fresh coremia of *Ceratostomella ulmi*

Fransen (1934) also called attention to mites as a factor in the transmission of *C ulmi*   A mite *Pseudotarsonemoides innumerabilis* Vitzth) is associated with the beetles in Holland   The mites, when present, disseminated the spores within the brood galleries and stimulated more profuse sporulation in the pupal chambers, thus increasing the effectiveness of the beetles as vectors

Mites as Vectors of Microorganisms Causing Decay of Plants. Woods (1897) described the action of the bulb mite (*Rhizoglyphus hyacinthi* Boisd) (Fig 181) on the Bermuda lily   The mites were found in large numbers on decaying roots and bulbs   By colonizing the mites on healthy plants, it was shown that they would attack uninjured tissues, which were soon destroyed by fungi and bacteria introduced by them   No detailed study was made of the fungi and bacteria responsible for the decay

Hodson (1928) has more recently studied the bionomics of the same mite (referred to as *R echinops* Fumouze & Robin)   He concludes that the bulb mite is not a primary parasite of uninjured hyacinth bulbs   In an extensive series of experiments, bulbs were infested with the mites under various conditions   If the bulbs were injured mechanically or by nematode infestation, they were rapidly destroyed by the mites and associated microorganisms, whereas control plants kept free of mites were not destroyed   It was further concluded that "the mites can undoubtedly carry fungus spores from bulb to bulb "

McDaniel (1928) in describing the injury caused by the bulb mite on hyacinths states "It is an accepted fact that otherwise

healthy bulbs infested by this species are subject to rot   As the disease develops and the bulb becomes soft, the hypopus stage of the mite appears, and migration to healthy bulbs takes place by means of some of its well known carriers   These healthy bulbs in turn become soft and rot "

Garman (1937) has studied the life history and activity of the bulb mite and reported experiments in which rotten bulbs containing mites were placed in pots of soil just below healthy bulbs The mites readily migrated from the rotten bulbs and infested the healthy ones, causing them to decay (Fig 182)   Welsford
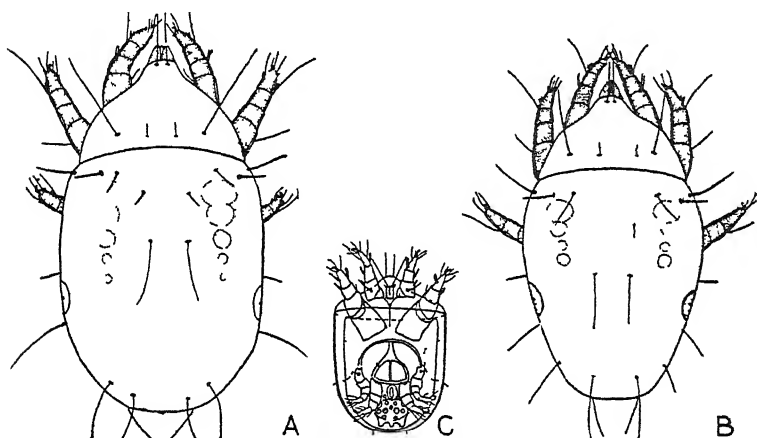
Fig 181 —The bulb mite   *A*, adult female, dorsal view, *B*, adult male, dorsal view, *C*, the hypopus, ventral view showing the ten suctorial organs by means of which the mite attaches itself to insects to be transported to new localities Approx 80 ×   (*After Garman*)

(1917), who investigated a bulb rot of narcissus in England, concluded that the nematode [*Tylencus* (*Anguillulina*) *dipsaci*] was more important as a vector than the bulb mite   The microorganisms responsible for the decay of narcissus bulbs have never been studied intensively, and it is probable that more than one disease is involved

The narcissus fly (*Eumerus tuberculatus*) and other insects play an important part in the distribution of the bulb mites which, in the hypopial stage, attach themselves to various parts of the insects' bodies and are distributed by the flies as they travel from bulb to bulb (Fig 183)   The mites are distributed also by many other insects that infest decaying bulbs under conditions

that would be conducive to the dissemination of bacteria or spores of pathogenic fungi

According to Taubenhaus (1913), black rot of sweet potato, caused by *ceratostomella fimbriata* (E and H) Sacc , is transmitted from root to root in the storage cellar by mites and red spiders (specific identity not given)   It was stated that when these arthropods were transferred from diseased to healthy roots the disease always followed   A pure culture of the pathogen was
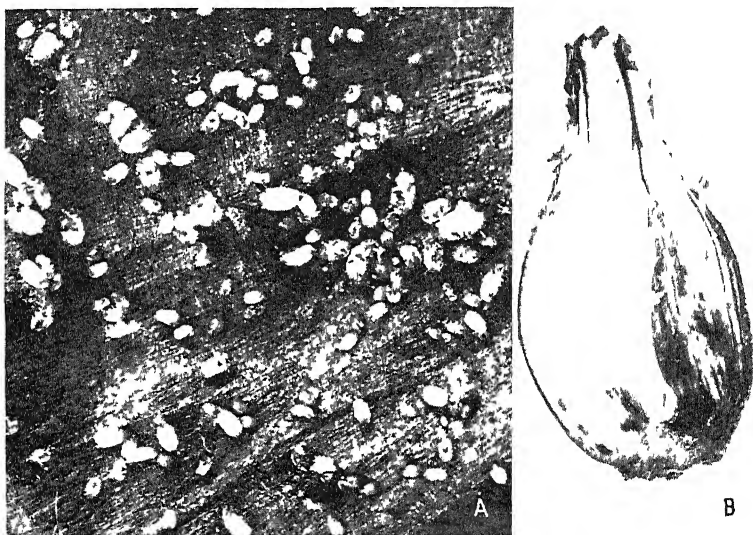
Fig 182 —*A*, mites feeding on a bulb scale, *B*, a hyacinth bulb infested with mites and beginning to decay as a result of inoculation of the tissues by the feeding mites   (*After Garman*)

isolated when the mites were taken from diseased roots and allowed to crawl over a poured plate of culture medium

Mites of various kinds are commonly associated with decaying plants where they are generally referred to as scavengers   This preconceived idea of the nature of their activity together with the known fact that they are wingless has tended to discount their possible significance as vectors of plant diseases   Certain dipterous insects, long known to be associated with decaying plants and generally considered to be scavengers only, have been shown to be important vectors of the microorganisms causing the decay (Leach 1926, 1927), and it is not improbable that some of the mites now classed as scavengers may prove to

be active vectors of pathogenic microorganisms   Moreover, some of these mites are tyroglyphids and are disseminated by flies and other winged insects that feed on decaying tissues   Therefore, the fact that the mites are wingless does not preclude the possibility of their action as vectors   There is need for more thorough study of the significance of mites as vectors of microorganisms that cause rotting of plant tissues

Fig 183 —Two flies (*Scatopse pulicaria* Loew) that breed in decayed bulbs, with hypopi of the bulb mite clinging to them   Approx 11×   The flies transport the mites to healthy bulbs and the mites in turn transport the fungi that are responsible for the decay   (*After Garman*)

Mites as Vectors of "Reversion" in Black Currants —Reversion, a destructive virus disease of black currants, prevalent in England and in Western Europe, is said to be transmitted by a mite [*Eriophyes ribis* (Westw) Nal] (Amos and Hatton, 1927, 1928)   This mite (Fig 173) is also the cause of the condition on currants known as "big bud" in which the buds become much enlarged but fail to open and eventually die   The mites then migrate to new buds and start new infestations   Big bud is not a symptom of reversion but is a distinct manifestation of mite infestation   Reversion is characterized by leaf abnormalities, dwarfing, and sterility   It can be transmitted by grafting but is not transmitted by artificial sap inoculation or

by the seed   For a somewhat more complete discussion of this disease and its vector, see Chap IX

NEMATODES

Nematodes, or roundworms, belong to the phylum Nemathelminthes and include many species parasitic on plants or animals

Left   Right
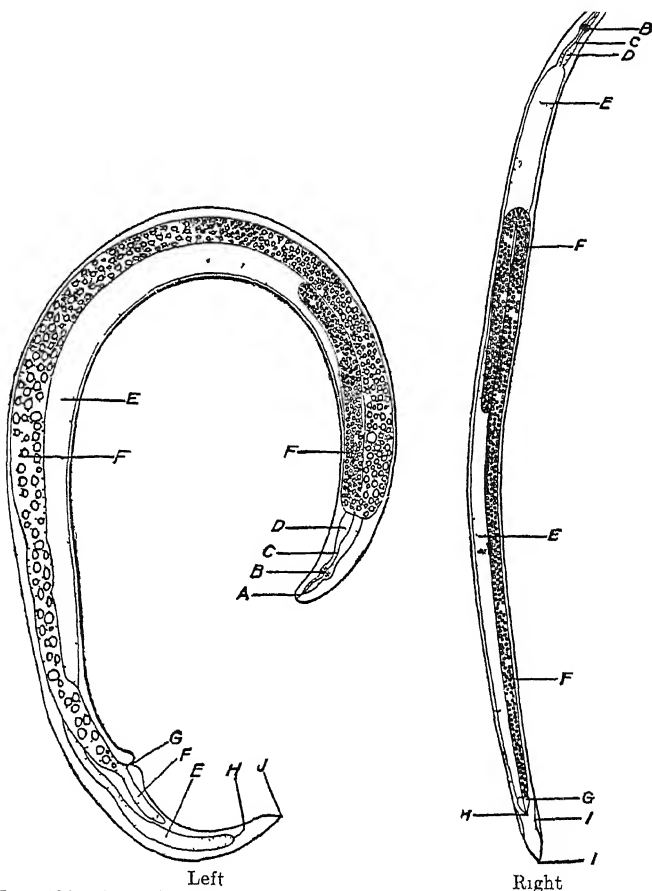
Fic 184 —*Tylenchus tritici,* a nematode causing a gall of wheat   Left, lateral view of a young female, right, a ventral view of a young male, *A,* spear, *B,* anterior esophageal bulb, *C,* esophageal canal, *D,* posterior esophageal bulb, *E,* digestive system, *F,* reproductive system, *G,* spicula in male and vulva in female, *H,* anus, *I,* bursa of male, *J,* tail   (*After Byars*)

as well as free-living saprophytes   Some species that affect animals are relatively large, often attaining a length of several

feet, but those affecting plants are small, usually not more than a few millimeters in length   These are often referred to as "eelworms "   The anatomy of nematodes is relatively simple (Fig 184)   They have elongated, spindle-shaped bodies   The mouth, provided with hook or stylet in the buccal cavity, leads into a muscular esophagus which serves as a suctorial pump   The intestinal tract is usually a straight tube   The body wall is muscular and is not segmented but is often transversely marked with rings of stiff cuticle   The nematodes move by a characteristic undulatory movement

FIG 185 —Photographs of the anterior end of the root-knot nematode, *Heterodera marioni* showing the action of the mouth parts   *A* showing the stylet protruding into the media, *B*, showing the extrusion of saliva, *C*, showing the mouth parts with the stylet fully retracted   (*After Linford*)

A nematode of the common plant-infesting species is equipped with a minute, hollow axial stylet, or spear, by means of which it pierces the cell walls of infested plants (Fig 185)   As a rule, the nematodes work their way into the tissues through the intercellular spaces   Usually they remain in the intercellular spaces and feed by piercing the cell walls with their stylets and sucking out the cell fluids   Digestion of the cell contents is aided by the injection of saliva through the hollow stylet   The method of feeding of the root-knot nematode (*Heterodera marioni*) has been described clearly by Linford (1937)   For a more detailed description of nematodes parasitic on plants and discussion of the diseases caused directly by them, the reader is referred to the treatise by Goodey (1933)

Nematodes and the Dilophospora Disease of Cereals —This is an association of two distinct diseases of cereals, a seed gall caused by a nematode [*Tylenchus tritici* (Steinbuch) Bastian] and a leaf-spotting disease caused by a fungus [*Dilophospora alopecuri* (Fr) Fr]   In Europe, the two diseases are usually associated   The nematode galls may occur independently of the fungus disease, but the fungus disease is rarely found on plants not affected with nematodes   The association of the two pathogens has been investigated extensively by Atanasoff (1925) who speaks of it as "coparasitism "   He concludes that the fungus disease is dependent upon the nematodes for its transmission and development but that it has a detrimental effect on the nematodes and the disease caused by them

The nematode (*T tritici*) (Fig 184) infects the developing ovaries and causes characteristic globular galls that replace the normal seeds of the affected plants   In each gall are found 10,000 to 15,000 dormant nematode larvae   The galls fall on the ground at harvest or may be planted later with the seed   As soon as the galls come into contact with the moisture of the soil, the nematode larvae become active, leave the gall, and wander through the soil to the nearest host plant   They instinctively find their way into the space between the leaf sheaths of the young cereal plants where they live as ecto-parasites   Gradually they work farther and farther between the leaves toward the center until they finally reach the growing point   As the plant grows and the internodes elongate, the nematodes are carried passively upward by the elongating stem   As soon as the head is differentiated, the immature nematodes bore into the young ovaries where they produce sexually, giving rise to thousands of young larvae in each gall   As the plant matures and the tissues become dry, the galls harden and the larvae become dormant, thus completing the life cycle

The fungus (*D alopecuri*) causes numerous dark spots, blotches, and stripes on the upper leaves and on other parts of the plant   Spores are formed in great numbers in pycnidia localized in the spots   In the early stages of infection, the fungus grows in between the folded leaves, binding them together so that the developing head cannot escape and is badly deformed and distorted   The nematode galls also become infected with the

fungus, Atanasoff being unable to obtain any galls completely free of *Dilophospora*

The spores of *Dilophospora* are cylindrical with tufts of bristlelike appendages at one or both ends (Fig 186) They are approximately 12 microns in length, exclusive of appendages, and 2 2 microns in width The appendages are 5 to 10 microns
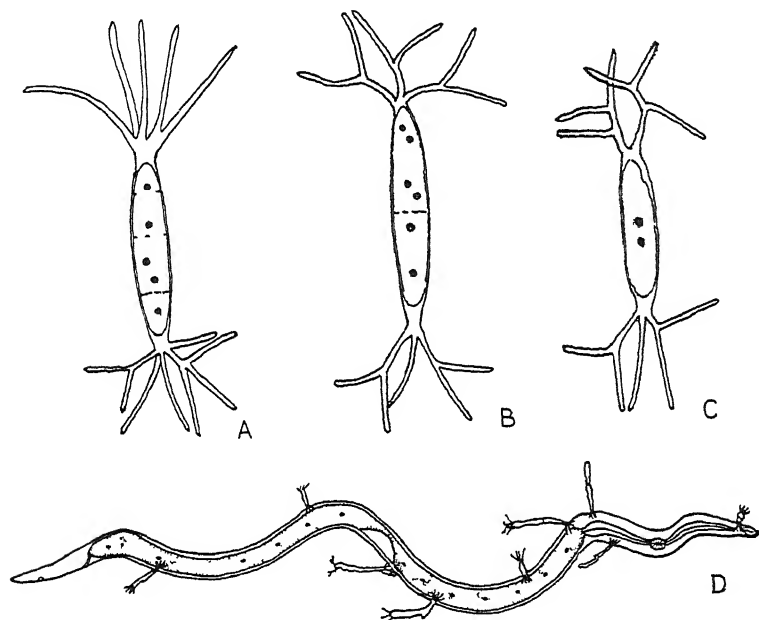
Fig 186 —*Dilophosphora alopecuri A*, *B*, and *C*, spores showing the setae by which they adhere to the nematodes, *D*, a nematode with spores of *Dilophospora alopecuri* adhering to it illustrating the method by which the spores are transported in between the unfolded leaves to the growing point were they germinate and infect the very young leaves   (*Redrawn after Atanasoff*)

in length and about 0 5 micron in diameter at the base   They are either simple or branched

When the nematodes in the galls become active, the fungus also begins to grow and to form spores which become attached to the body of the nematode larvae by means of the bristles as shown in Fig 186*d*   In this way, the spores are transported by the nematode larvae into the intersheath spaces and to the young growing point   Here some of them germinate and infect the very young leaves   The symptoms, however, do not

become noticeable until the leaves have unfolded   Nematodes taken from near the growing point of wheat plants always carry numerous spores attached to their bodies

When spores were artificially introduced into the plant near the growing point in the absence of nematodes, the disease was not produced   Atanasoff explains his inability to produce the disease by artificial inoculation in the following way   That which was a growing point a few days or even hours ago is now a leaf   The spores introduced artificially in the absence of nematodes are soon pushed upward and outside onto older tissue where infection does not take place   The nematodes avoid this fate by continuously deserting the newly differentiated leaves and moving constantly downward to the undifferentiated tissues of the growing plant

The nematodes not only bring the Dilophospora spores into the central cavity of the plant and carry them subsequently back to the growing point of the plant from its growing out leaves, but the nematodes, sucking or otherwise injuring or affecting the plant cells of the tender and minute leaves, open the way for the penetration of the fungus into the cells and tissues of the leaves and afterwards of the young head

Additional support of this explanation is furnished by the fact that plants already infected with *Dilophospora* will completely recover and produce normal leaves as soon as the nematodes die, as they sometimes do   It is also noteworthy that the lower and older leaves are never infected by the fungus

Schaffnit and Wieben (1928) have questioned the importance of the nematodes in the development of this disease   By inoculating the very young tissues of germinating seed with a suspension of *Dilophospora* spores, it was shown that the fungus could infect wheat and rye plants in the absence of nematodes   The conditions that resulted in artificial infection were, however, not entirely typical of the conditions that influence the development of the disease as it occurs in nature

It is apparent that we are dealing here with a fungus disease of cereals that is transmitted by a nematode, itself a cause of disease on the same plant   Although the fungus may infect its host plant and survive in the absence of the nematode, it apparently is more effective as a pathogen when associated with the nematode that transports the spores to the delicate

tissues of the growing point   The spores are ensured of trans-
portation by virtue of the bristlelike appendages that adhere
readily to the mucous covering of the nematodes   In so far as is
known, the nematodes derive no benefits from the association

**Root Nematodes as Agents of Transmission of Plant Patho-
gens**—There are numerous nematodes that infest the roots of
plants   Many of these such as the root nematodes *Heterodera
marioni* and *H schachtii*, cause destructive diseases independently
of pathogenic fungi or bacteria   Others are aided in their
destructive activity by pathogenic microorganisms which are
introduced into the plant tissues by the nematodes   There
are many reports in the literature of observed associations of
nematode infestations and pathogenic microorganisms, but very
few of these have been studied in detail   The majority of the
reports deal mainly with observations unsupported by careful
microscopic examination and experimental evidence, although
there are some exceptions

One of the more recent reports is that of Kalinenko (1936),
who has shown that in Russia three species of nematodes (*Tylen-
chus multicinta* Cobb, *T pratensis* de Man, and *Aphelenchus
avenae* Bost) attack the roots of two rubber-bearing plants and
inoculate them with *Erwinia carotovora* and several other species
of bacteria   The combined actions of the nematodes and
bacteria are destructive to the plants

Careful microscopic examination showed clearly that the
bacteria were inoculated into the root tissues by the nematodes
It was demonstrated by cultural studies that the bacteria were
transported both internally and externally by the nematodes
and that the bacteria, having gained access to the root, caused
extensive destruction of the tissues independently of the action
of the nematodes

What is apparently a similar association between nematodes
and a fungus has been reported by Triffit (1931) from England,
where the nematode *H schachtii* is often a destructive pest of
potatoes causing a condition referred to as "potato sickness"
It was observed that plants in certain areas in a field often are
more severely injured than plants in other areas which are equally
as heavily infested with nematodes   It was concluded that
when nematodes were the only factor concerned, very little
harm was done, the severe injury being caused by the combined

action of the nematodes and a fungus (*Colletotrichum atramentarium*)   No detailed histological or cultural study was made of the association

Millikan (1938) has studied the eelworm disease of cereals (*H schactu* Schmidt) in Australia   He comments that "root-rot fungi occur freely in association with eelworms   particularly in wheat and in some instances at least, these undoubtedly have been the major cause of poor growth "

It is only reasonable to expect that when plant roots are invaded by nematodes, the resulting wounds would often serve as entrance points for soil fungi or bacteria which are to some extent pathogenic   In most cases, the injury caused by the relatively inconspicuous fungi or bacteria has been attributed to the activity of the more obvious nematodes   There are numerous examples of nematode injury in which fungi have been observed to be involved to some extent   A few of the better known ones will be mentioned briefly

The root-knot nematode [*H marioni* (Cornu) Goodey] has long been recognized as a contributing factor in the development of fusarium wilt of cotton   Wilt is always more severe on soil infested with nematodes than on noninfested soil (Young 1928, 1938, Rosen, 1928), and it has been observed that the most wilt-resistant cotton varieties may become very susceptible in nematode-infested soil   The mechanism by which the resistance is broken down is not known, although it is assumed that the more effective inoculation resulting from nematode attack is the determining factor   Rosen states

> The action of nematodes on roots is largely that of producing localized, hyperplastic overgrowths, consisting mostly of soft, parenchymatous tissue and a reduced amount of cork and wood   It seems reasonable to assume that this production of soft, succulent tissue offers an excellent opportunity for the growth of the cotton-wilt parasite, and this appears to be the explanation for the prevalence of cotton wilt on nematode-infested soil

Arndt (1935) has reported that damping off of cotton seedlings often follows invasion of the roots by nematodes   He states that the nematodes alone, in the absence of fungi and bacteria, are unable to cause damping off

The eelworm disease of potatoes caused by *Anguillulina dipsaci* Kuhn is often destructive in England and Holland   The tubers

are affected, the injury closely resembling that caused by late blight According to Goodey (1933), "As a rule a general putrefactive rot sets in and spreads throughout the tubers when these are lifted and clamped, consequently where the disease is found the crop should be disposed of and not stored in clamps " The direct cause of the decay in this case has not been studied extensively

The same nematode also affects narcissus bulbs, and it is stated (Goodey 1933) that "diseased bulbs are rapidly attacked by many other secondary invading organisms including saprophytic nematodes, bacteria, mites, moulds, and fly larvae, etc , till finally a rotting mass is produced within the outer dry scales " Welsford (1917) has studied a destructive bulb rot of narcissus associated with infestation of this nematode He concluded that the nematode is of greater significance as a vector of decay than the bulb mite

The burrowing nematode [*A similis* (Cobb) Goodey] has been shown by Muir and Henderson (1926) to be associated with a root rot of sugar cane in Hawaii The nematode attacks the sugar-cane roots near the tips, terminating the growth and causing excessive formation of laterals which are in turn infected The affected parts become red, then brown, and finally purplish black A fungus is constantly associated with the nematode attacks and, when cultured, produces the same color on artificial media that is found in the affected roots

Anguillulina (*Tylenchus*) *pratensis* de Man is a nematode that attacks the roots of many different kinds of plants It is injurious to cereals in Germany and other regions where it has been studied extensively According to Goodey (1933), the injury is caused not so much by the direct action of the nematode as by the fungi which attack the roots weakened by the nematode, but no careful study of the associated fungi has been made Steiner (1927) has described and pictured this nematode in the roots of various plants (Fig 187) He states that "specimens of *Tylenchus pratensis* undoubtedly move slowly but continually through the root tissues The path prepared by the larvae aids in the spread of other root diseases through the root tissues, especially fungi Cases have been observed by the writer where numerous chytrids could be seen following what appeared to be the trail of *T pratensis* "

It will be seen from the preceding discussion that the relationship between nematodes and plant pathogens is in need of further study   The general problem of nematodes and associated fungi and bacteria has been stated by Goodey (1933) as follows

Because we sometimes find nematodes associated with unhealthy conditions of plants and are unable to assign the disease to some par-

FIG 187 —Nematodes in roots   A, *Tylenchus pratensis* in a root of a wheat plant (approx 55×), B, T *pratensis* in a root of lily of the valley (approx 60×)   (*After Steiner, by courtesy of the U S Dept Agr*)

ticular pathogenic organism, we may be inclined to conclude that the nematodes found are causally related to the diseased conditions   This is scarcely warrantable without a thorough search for other possible sources of disease of a fungal, bacterial, virus, or physiological nature The whole subject is one calling for much further investigation since at the present time, apart from our knowledge of the obligate parasites, we have but little exact information on the part played by other kinds of nematodes in the microbiology of the soil or in relation to the plant in health or disease

EARTHWORMS

Earthworms and Clubroot of Crucifers —Gleisberg (1922) has reported evidence to show that earthworms are concerned in the spread of clubroot of crucifers, a disease caused by a fungus (*Plasmodiophora brassicae* Woronin) Large irregular swellings develop on the roots of affected plants Spores are formed within the cells of affected tissue and are liberated only after the plant dies and the roots decay The spores germinate in the soil and form myxamoebae that find their way to the roots of new plants which they infect through the root hairs Although infested areas of soil do not increase in size rapidly the rate of spread is often faster than can be explained by the direct migration of the fungus in the soil

Gleisberg placed 3 to 10 earthworms in pots of infested soil and allowed them to remain for 1 month, then removed them to new pots of disease-free soil which he planted to cabbage Sixty per cent of the plants were infected in these pots, whereas none were infected in similar pots of noninfested soil to which no earthworms were added The pathogen, in virulent form, was found to be abundant in the excreta of the worms, and it was concluded that earthworms in nature would carry the spores of *P brassicae* for some distance in the soil It was shown that deep plowing to turn under the infested soil is of only temporary value, because the earthworms soon bring enough of the inoculum to the upper layers to reinfest it

The dissemination of *Plasmodiophora* in this way would be relatively local, because earthworms do not travel for very great distances There is a possibility that they may be indirectly responsible for long-distance transmission by birds that feed upon earthworms There is no experimental evidence, however, to show that this ever occurs

SLUGS

On several occasions, slugs have been reported as agents of dissemination of fungus spores or bacterial plant pathogens, but as a rule they are of relatively little importance as vectors of plant diseases As early as 1896, Wagner reported experiments with slugs (*Helix hortensis* Mull , *Succinia putris* L , and *Arion subfuscus* Drap) showing that they effectively dissemi-

nated spores of several species of pathogenic fungi   The spores were disseminated both externally in the slime and internally in the fecal excretions   The spores of all species of fungus tested passed through the intestinal tract of the slug uninjured, and such spores were virulent when tested by artificial inoculation   In a number of experiments, slugs were starved for several days, then allowed to feed, first on diseased plants, then later on healthy plants to which the diseases were transmitted [*Plasmopera nivea* (Unger) Schroeter on *Aegopodium podagraria* L , *Bremia lactucae* Regel on *Sonchus oleraceae* L , and *Peronospora parasitica* (Pers) on *Dentaria bulbifera* L and others]   In no case, however, was it shown that the transmission by slugs was of major importance in the spread of the disease in nature

Smith (1897) has reported successful transmission of black rot of cabbage [*Phytomonas campestris* (Pammel) Bergey *et al*] by slugs, but this method of transmission is of little significance in nature   Buller (1909) has reported that many slugs feed on the fruiting bodies of the fleshy fungi, ingesting large quantities of spores   He reviews the work of Voglino who found germinating spores of several species of the Hymenomycetes in the intestinal tracts of slugs   Toads that feed on slugs also harbor viable fungus spores in their intestines   Voglino believed that the slugs played an important role in the propagation of the fungi by providing suitable conditions for spore germination   Buller, on the other hand, more logically concludes that "although it may be true that slugs help in the local dispersal of spores in a wood or field and provide conditions for their germination, these animals, owing to their slow rate of movement, could scarcely act as agents in spreading fungus species from wood to wood when they are separated by considerable distances "

Giavatt and Marshall (1917), in an experimental greenhouse test, observed slugs eating the teliospores of *Cronartium ribicola* and demonstrated that some of them were viable after passage through the digestive tracts of the slugs, but there was a marked decrease in the percentage of spores that germinated   It was concluded that these animals were of relatively little practical importance as vectors of the disease

Similar observations on the dissemination of cereal-rust spores by the imported garden slug (*Agriolimax agrestis*) were reported

by Gianovsky and Levine (1932)   Slugs that had been allowed to feed on rust pustules in the greenhouse were placed on healthy seedlings   Rust infection invariably appeared along the trails of the slugs as marked by the mucous secretion   Infection was obtained also by using the excreta and intestinal contents of slugs as inoculum   The spores were apparently uninjured by passage through the slugs, but the latent period of the rust was somewhat prolonged   Transmission of rust by slugs in the greenhouse might be of significance from the standpoint of experimental work but would be of little significance in the epiphytology of cereal rusts in nature

BIRDS

From time to time, various workers have expressed the opinion that birds are important vectors of certain plant diseases   However, there has been relatively little careful study of the question   The most complete investigation of the subject on record is the study of Heald and Studhalter (1914), dealing with birds as vectors of the chestnut-blight fungus   These workers made a study of the spores carried on the bills, feet, and feathers of 36 birds belonging to nine different species   All the birds examined were shot on infested chestnut trees   The species represented in the study are as follows   (1) the hairy woodpecker (*Dryobates villosus*), (2) the downy woodpecker (*D pubescens medianus*), (3) the junco (*Junco hyemalis*), (4) the flicker (*Colaptes aureatus luteus*, (5) the white-breasted nuthatch (*Sitta carolinensis*), (6) the brown creeper (*Certhia familiaris americana*), (7) the golden-crowned kinglet (*Regulus satrapa*), (8) the sapsucker (*Sphyrapicus varius*), and (9) the black-and-white creeper (*Mniotilta varia*)   Of these, the hairy woodpecker and the flicker were the only ones not found carrying spores of *Endothia parasitica*, the blight pathogen   Of the 36 birds examined, 19 were found to be carrying spores of the fungus   The estimated numbers of viable spores carried by two downy woodpeckers were 757,074 and 624,341, respectively, and a brown creeper carried 254,019 viable spores

The old cankers of chestnut blight are frequently infested with bark-boring insects as pointed out by Craighead (1916), and the birds often riddle the cankers in search of the insects   Such a riddled canker of chestnut blight is shown in Fig 188   In this

way, the birds become thoroughly contaminated with spores of
the fungus

The birds, killed 2 to 4 days after a period of rainy weather,
always carried more spores than those killed in dry weather
The spores carried were all pycnidiospores, ascospores were
never found on the birds   The authors conclude that birds
are important vectors of the fungus but that because of the pre-
dominance of wind dissemination of ascospores they are not of
great significance in local spread   They believe, however,
that they are responsible for the so-called "spot" infections at
some distance from areas of general infection
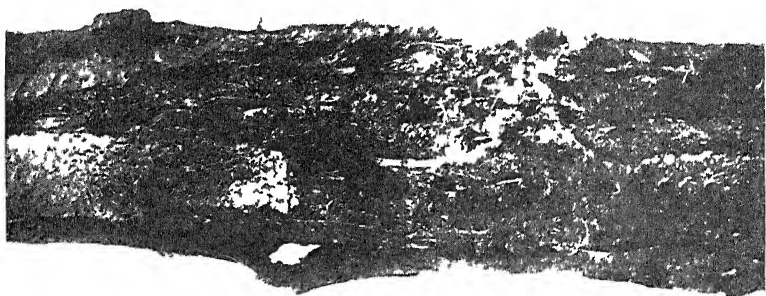
Fig 188 —A chestnut canker that has been riddled by birds while feeding on
insects under the bark   Birds became contaminated with the spores in this
way and aided in the dissemination of spores over long distances   (*After Heald*)

Inasmuch as the birds involved in the study are migratory,
they are potentially important vectors for long-distance spread
of the fungus   It is entirely possible that by starting new centers
of infection they contributed materially to the rapid spread of
chestnut blight throughout the range of the chestnut forests
in this country

The extent to which these birds actually transmit the disease
depends largely upon the opportunity they have for inoculating
healthy trees   Heald and Studhalter (1914) state that "each
time the bird climbs or creeps over the trunk or limbs of a tree
some of the spores may be brushed off and may lodge in crevices
or on the rough bark   From this position they may be washed
down into wounds by rain and may thus cause infections "
A still more effective method of inoculation not mentioned by

these authors is provided by the habit many of these birds have of feeding on the cambium of healthy trees. Nearly all the woodpeckers and sapsuckers that feed on bark-boring insects also include fresh cambium in their diet (Roberts 1932). The wounds made in the bark of healthy trees would be ideal infection courts, and if the bird had fed recently on insects from a spore-laden canker, infection would follow almost certainly.

Birds (woodpeckers and sapsuckers) that feed on the elm bark beetles in elm trees infected with the Dutch elm disease have been suspected of transmitting the disease, but no careful study of the subject has been reported. In view of the migratory nature of these birds and their habits of feeding on fresh cambium as well as on the insects from infected trees, it is very likely that they may be responsible for starting centers of infection at some distance from the known area of general infection. Transmission by bird vectors may offer a possible explanation of the few reported cases of trees infected with the Dutch elm disease in the absence of beetle infestation.

Birds as Vectors of Mistletoe.—The mistletoes cause well-recognized diseases of forest trees. They rarely, if ever, kill a tree, but they often do cause severe malformation, sap the vitality of the tree, and greatly reduce its rate of growth. The mistletoes are semiparasites which derive part of their nourishment from the sap stream of living trees. The xylem vessels are tapped by rootlike haustoria through which they withdraw water and mineral salts in solution. They are not dependent upon the tree for carbohydrates, because they possess chlorophyll and are able to synthesize their starch.

The mistletoes are seed-bearing plants (Fig. 189) and are transmitted from tree to tree entirely by seeds which are disseminated largely by birds. The role of birds in disseminating mistletoe has been described by Bray (1910). The seed of the mistletoe, when ripe, is enclosed in a clear, sticky pulp covered by a semitransparent skin. The sticky pulp is clearly an adaptation for seed dispersal. The seed and its covering, constituting the berry, are utilized as food by several species of bird. The mockingbird, the cedar waxwing, and the robin are among the most important birds that feed upon the berries, disseminating the seeds. The birds ingest the seeds and may either pass them out in excrement or regurgitate them. The seeds also adhere

readily to the feet or to the beak, later to be wiped off on a branch
The seeds by virtue of their sticky coating adhere to the branches
and in moist weather germinate and infect the tree   The seeds
are obviously poorly adapted to wind dissemination

Bray has observed that the point of first infection on a tree
often is determined by the perching habits of the birds that
feed upon the berries   Large areas were noted in which there
was a predominance of cases where a single plant of mistletoe

Fig 189 —A female plant of western dwarf mistletoe, with mature berries
on ponderosa pine   The sticky pulp of the berry causes the seed to adhere to
tree branches, where they germinate   They also adhere to the feet and beaks of
birds and may be transported long distances by them   (*After Boyce*)

grew from a point near the apex of the topmost branch, a choice
perching place of the mockingbird   This point of primary
infection is ideal for further infection of the lower branches by
falling seeds

The dwarf mistletoes, which cause destructive diseases of
conifers in Western North America, also produce their seed in a
sticky matrix   On maturity, the berries develop a strong internal
pressure which slowly increases until a slight disturbance causes
them to explode, forcibly ejecting the seed for a distance of
several feet   The sticky coating causes them to adhere to the
surrounding branches on which they may fall   Local dissemina-
tion is accomplished in this way, but for dispersal over longer

distances dependence must be placed upon birds   The birds
transport these seeds in the same ways that they transport the
seeds of the true mistletoes

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CHAPTER XII

THE ANATOMY AND PHYSIOLOGY OF PLANTS IN RELATION TO INFECTION AND INSECT VECTORS

In the process of evolution, plants have developed a number of natural defenses against unfavorable environmental factors, insect pests, and infection by microorganisms. At the same time, the pathogenic microorganisms and insect pests have evolved means of overcoming to some extent these protective adaptations. The end result has been a certain degree of equilibrium in the struggle, involving the interaction of plant, pathogen, and insect. In order to have an adequate concept of the role of insects in the development of plant diseases, it is necessary to consider in some detail the natural defenses of plants, as well as the ways in which the pathogens or insects overcome or circumvent them. Only in this way can we properly evaluate the part played by insects in the processes of infection.

The plant should be visualized as a living organism composed of a number of delicate tissues that must be protected against the vicissitudes of both the living and nonliving environment. Each tissue and each cell of the plant have a number of functions to perform, and their nature is usually determined by their functions. Since protection is only one of the many functions of plant tissues, compromises have been necessary so that perfect protection has never been achieved. Chief among the living components of the environment, against which protection is necessary are insects and pathogenic microorganisms. In this chapter, certain tissues and physiological processes will be considered from the viewpoint of their influence upon the susceptibility of plants to the attack of microorganisms or insects, or both combined.

The Epidermis —In the early stages of growth, the entire outer surface of any higher plant is covered with a single layer of specialized cells, the epidermis (Fig 190). The epidermis forms a complete covering except at a few points such as the stomatal

openings, hydathodes, and nectary glands and in the growing points where the cells are still meristematic, the epidermis not yet having been differentiated   The epidermis is made up of living cells, but all except the guard cells of the stomata are devoid of chlorophyll   With the exception of such specialized cells as root hairs and stomatal cells, the structure of the epidermal cells is designed primarily for protection   The outer and radial walls of
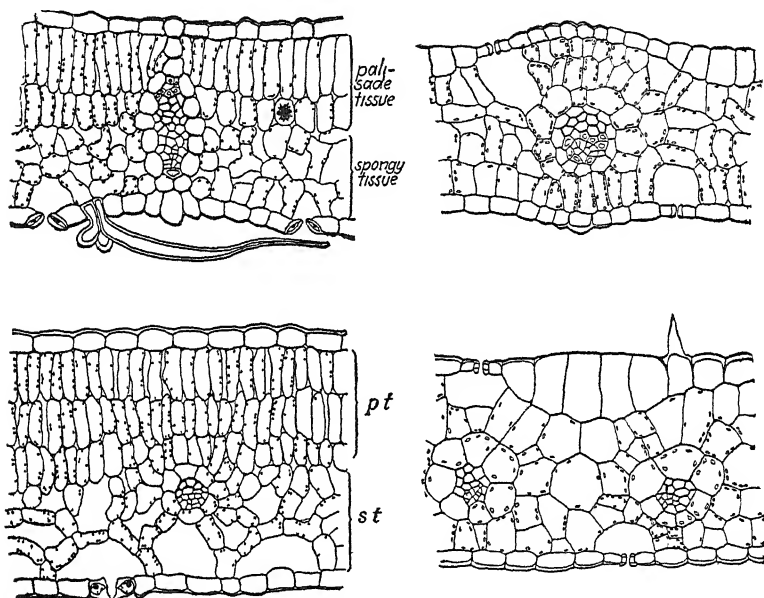
FIG   190 —Cross sections of leaves showing the epidermis and some of its protective features   Note the thickened outer wall and the arch or domelike curvature it forms   (*After Eames and MacDaniels*)

epidermal cells are often thickened to give strength and to resist mechanical injuries   The outer wall is curved to form a domelike structure that gives added resistance to pressure from without   Almost the entire surface of the epidermis, on the aerial parts of the plant, is covered with a layer of a waxy substance known as "cutin"   This is called the "cuticle" and constitutes a very effective barrier against infection by many microorganisms (Fig 191)   The cuticle is highly impervious to water and air and is resistant to chemical action   No enzyme is known that will dissolve it

A number of phytopathogenic fungi are able to penetrate the cuticle by mechanical means, others enter the plant through natural openings, but many depend entirely upon wounds Those which penetrate by mechanical means utilize the force of
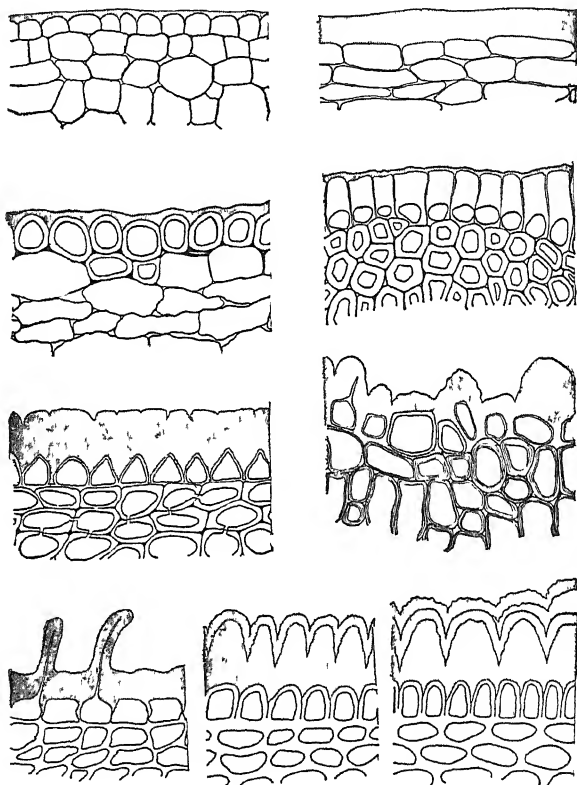
Fig 191 —Sections of the epidermis and adjacent tissues of several different plants showing the cuticle (shaded areas) The cuticle is composed of cutin, a substance highly resistant to chemical action Fungi are unable to produce enzymes that will dissolve it   (*After Eames and MacDaniels*)

growth pressure   The germinating spore forms a thick-walled spherical body closely appressed to the cuticle (Fig 192)   The entire protoplasm of the germinating spore is condensed into this "appressorium "   Growth is renewed at the point of contact of appressorium and cuticle, and a very thin hypha is pushed through the cuticle   After the cuticle is penetrated, the hypha

enlarges to normal size and continues to grow   This method of
penetration is common among certain groups of fungi, but the
majority of pathogenic fungi gain entrance in some other way

Wounds serve as the most important infection point for plant-
pathogenic bacteria   No bacteria are known that are able to
penetrate the plant through unbroken cuticle   With the excep-
tion of stomata, lenticels, hydathodes, the floral organs, and the
noncutinized root hairs, wounds are the only avenue of entrance
for the bacterial pathogens
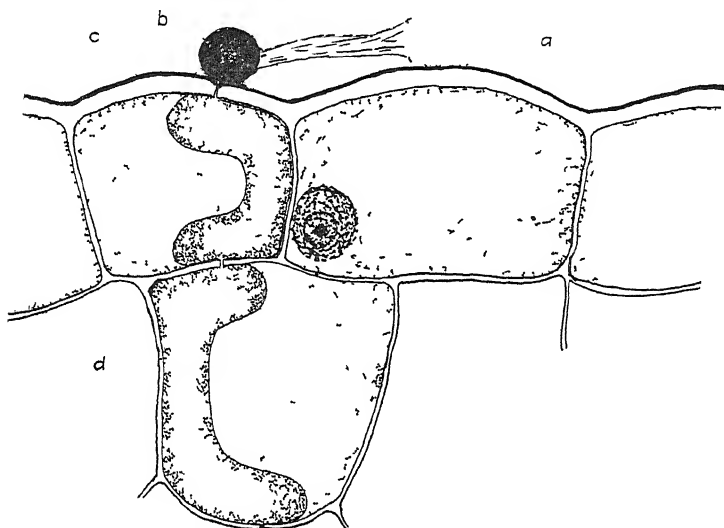
Fig 192 —A semidiagrammatic drawing showing the method of cuticle pene-
tration by *Colletotrichum lindemuthianum* the pathogen of bean anthracnose
a, Empty spore after germination, *b*, appressorium, *c*, cuticle of bean plants, *d*,
fungus mycelium in host cell

The cuticle is often covered with minute particles of wax, or
"bloom," which, because of its high surface tension, very effec-
tively sheds water, preventing it from wetting the surface of the
plant   Plants or plant parts that shed water readily usually
escape direct infection with greater frequency than plants that
wet more easily   Stomatal penetration by bacteria is also rare
on plants with a heavy bloom   This fact can be attributed to the
absence of a film of water connecting the surface of the epidermis
with the substomatal chamber   Such a film appears to be
necessary for stomatal infection by bacteria

Although the cuticle may serve as a barrier against pathogenic microorganisms, it is not always effective against the feeding and oviposition of many insects   A thick or tough cuticle, however, might easily discourage certain species of insects and cause them to show a preference for the varieties or species with a thinner
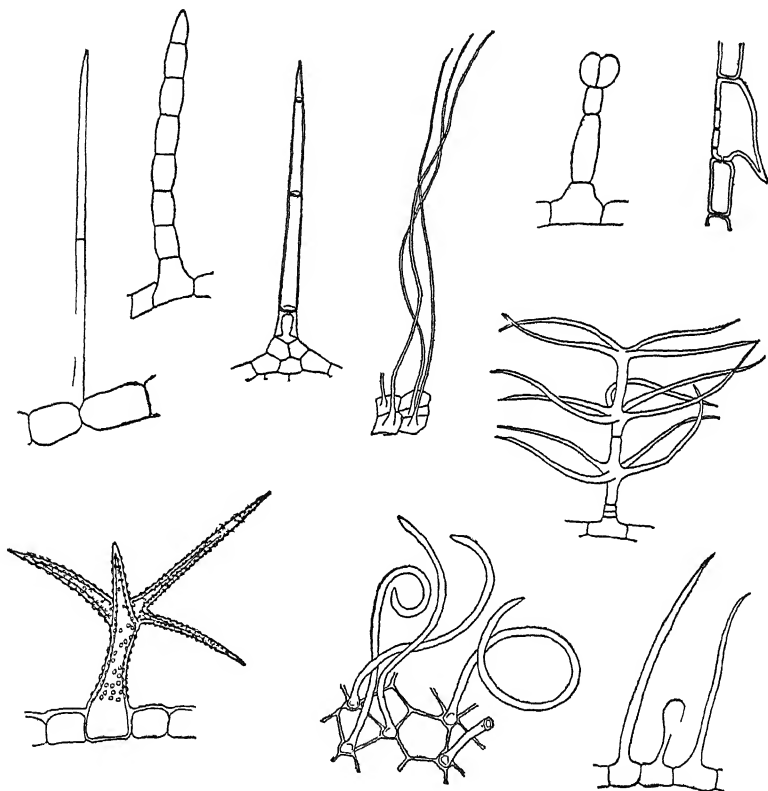
Fig 193 —Trichomes or plant hairs from several different kinds of plants These are all modified epidermal cells   They serve many different functions one of which is protection against insect and fungus enemies   (*After Eames and MacDaniels*)

cuticle   In such cases, if the insect were a vector of a disease, the nature of the cuticle would be an important factor in the ability of the variety to escape infection   Susceptible varieties that escape infection in this way are said to be "klendusic"   Numerous examples of klendusic varieties of crop plant have been reported, but for many of them no satisfactory explanation of the

disease-escaping qualities is known A study of the nature of the cuticle of such plants and its relation to the feeding and oviposition of insect vectors should be made

On many plants, certain epidermal cells are often modified in structure to form hairlike projections commonly known as "trichomes"(Fig 193) which vary widely in form and may serve different functions A plant with numerous trichomes is said to be "pubescent", one with few or none is "glabrous " The degree of pubescence of a variety often determines the extent to which certain insects will feed or breed on it When the size or abundance of the trichomes is sufficient to interfere greatly with the insects, they will avoid the pubescent varieties and seek the glabrous ones Consequently, the pubescent varieties often escape diseases caused or transmitted by the insects Perhaps the most striking examples are afforded by the pubescent varieties of clover reported by Hollowell, Monteith, and Flint (1927) and Monteith and Hollowell (1929) and the pubescent varieties of soybeans described by Johnson and Hollowell (1935) The pubescent varieties of these crops suffer much less from hopperburn, because the leaf hoppers [*Empoasca fabae* (Harris)], responsible for the burn, prefer the more glabrous varieties and feed and breed on them to the exclusion of the pubescent ones (Figs 55 and 56) A knowledge of this anatomical relationship should be of considerable value in breeding for superior disease-escaping varieties of these crops

A similar relationship between apple varieties and leaf-hopper injury has been reported by Schoene and Underhill (1937) These authors showed that "the susceptibility of apple varieties to leaf-hopper injury varied inversely with the amount of pubescence of the foliage " The recognition of the correlation of such visible characters with disease-escaping qualities should be of value in apple breeding as well as in the selection of varieties for planting in regions where leaf-hopper injury is prevalent

The Stomata —The openings in the epidermis, through which interchange of gases between the atmosphere and subepidermal cells occurs, are called "stomata" (Fig 194) These usually are well distributed over the surface of leaves and on the surface of green stems The stomata are necessary openings in the protective epidermis, but they are utilized also as the chief avenue of entrance by many disease-producing fungi and bacteria Many

pathogens, however, cannot infect in this way, even though the
inoculum may enter the stomata and reach the intercellular
spaces   Such pathogens usually require wounds for successful
infection   Where stomatal infection is the usual method, insects
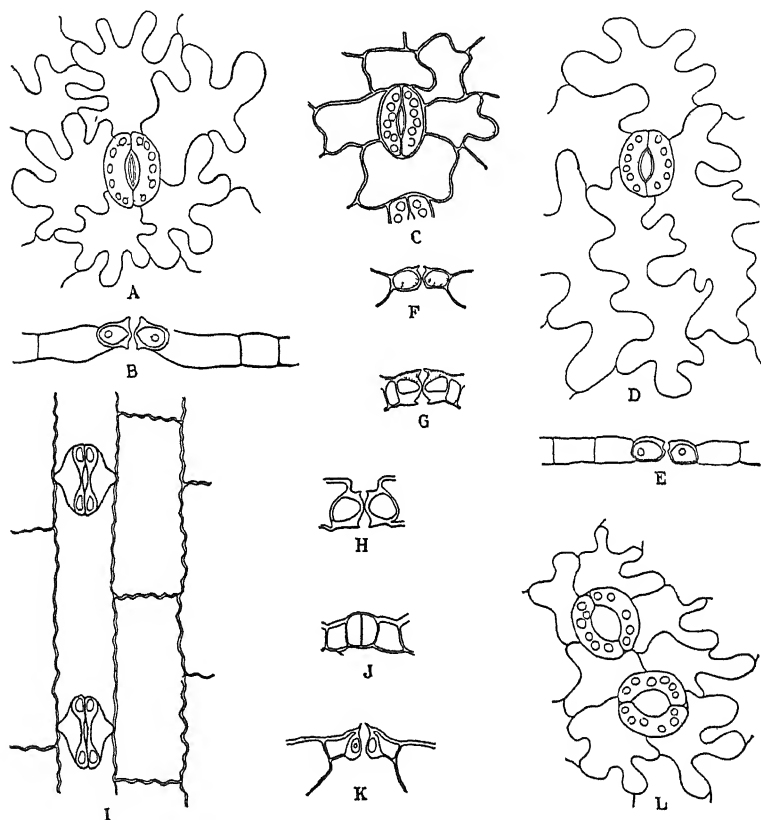
Fig 194 —Stomata of several different plants, *A, C, D, I,* and *L* in surface
view   *B C, F, G, H, J,* and *K* in cross section   Stomata are important avenues
of entrance for both fungi and bacteria   They are of no significance in insect
feeding   (*After Eames and MacDaniels*)

are of little importance in ingression, although they may be
important in disseminating the inoculum

The stomatal openings are so small that they have little or no
influence on the feeding of insects   Some are sufficiently large
to permit the insertion of the mouth parts of the smaller sucking
insects, such as aphids, but as a rule these insects show no prefer-

ence for the stomata   Their mouth parts are capable of penetrating the cuticle without difficulty and they usually follow the intercellular spaces of the underlying tissues

Stomata rarely serve as avenues of infection for the viruses, although Duggar and Johnson (1933) obtained a small amount of infection by spraying uninjured tobacco leaves with a suspension

FIG 195 —Plasmodesmata   Photomicrographs of cell walls of the tobacco plant stained to show the strands of protoplasm which connect the protoplasts of adjacent cells   *A*, *B*, and *C*, seen in cross section, *D* and *E*, surface view of the cell walls, *A* and *B*, 880×, *C*, 260×, *D*, 440×, and *E*, 1,020×   (*After Livingston*)

of the mosaic virus   Since the virus particles must come in contact with living protoplasm in order to infect, infection through uninjured tissues could be explained only by assuming that some of the virus particles reached the plasmodesmata

Plasmodesmata —In nearly all plant tissues, the protoplasts of the individual cells are connected with each other by fine strands of cytoplasm that pass through minute openings in the cell walls   These protoplasmic bridges are known as "plasmodesmata" (Fig 195)   There is considerable evidence to show

that certain viruses may spread from cell to cell through these structures   Drake *et al* (1934) have observed that aphids and other similar insects often introduce their setae into the walls between the cells and feed without puncturing the cells   It is suggested by these authors that the plasmodesmata serve as important structures in the infection of plants by viruses through the agency of aphids and similar insects

The Hydathodes —Under conditions of high humidity and low transpiration coupled with high soil moisture, plants often exude
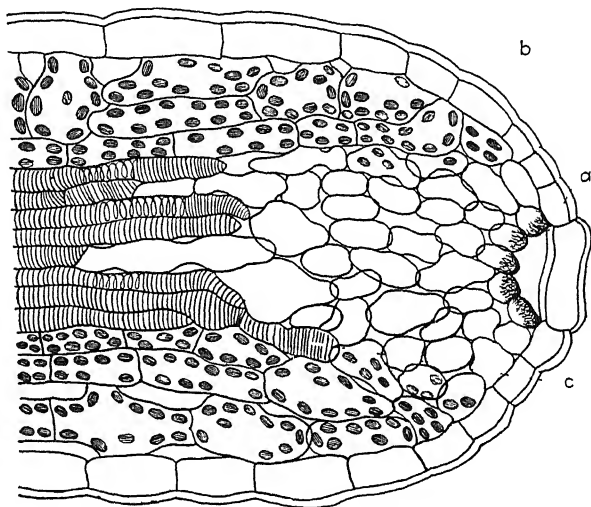
FIG 196 —A diagrammatic drawing of a section through a hydathode, or water pore, of a leaf   Note that the water pore is located near the end of a vein   Under conditions of high humidity, water from the vessels may pass through the intercellular spaces and be exuded in drops through the pore   *a*, pore, *b*, epidermis, *c*, terminal cell of a xylem vessel

water from the tips and margins of the leaves   The openings through which the water is exuded are called "hydathodes" or "water pores" (Fig 196)   They are located near the ends of the veins and are directly connected with the water-conducting vessels   The loss of water through the hydathodes is called "guttation," and the drop of water that is formed on the leaf margin over the hydathode is spoken of as a "guttation drop" (Fig 197)   Water of guttation is relatively pure although it usually contains a small amount of nutrient materials   Some plant pathogens, especially bacteria, may enter the plant through

the hydathodes   They first enter the guttation drop, where they may find nourishment sufficient to support growth and multiplication   As transpiration increases, some of the guttation water may be drawn back into the leaf, and the bacteria are drawn in with it   It has been observed that insects, especially flies, frequently visit and feed upon the guttation drops and in all probability introduce bacteria into them   This is said to be an important method of infection of cabbage by *Phytomonas campestris*, the black-rot pathogen (Smith 1911)   Hildebrand

FIG 197 —Cabbage seedlings growing in a humid atmosphere and bearing drops of guttation water

(1937a) has shown also that fire-blight bacteria may infect through the hydathodes of the sepals of apple blossoms

The guttation drops have been considered as a possible avenue of infection for virus diseases, but Caldwell (1930, 1931) has shown that a virus does not infect when added to the guttation drop unless the adjacent plant cells are injured   The virus particles appear unable to diffuse through an uninjured protoplasmic membrane   In a like manner, the guttation drops on a plant infected with a virus disease do not contain the virus unless the tissues have been wounded   It would seem, therefore, that hydathodes are probably of little significance as avenues of infection for virus diseases.

Nectaries and Other Floral Organs —Exposed tissues, poorly
or not at all covered with a cuticle, are found in the flowers of
higher plants   These unprotected tissues are usually susceptible
to direct infection by many pathogens   The nectary glands, the
anthers, and the stigmatic surfaces are especially favorable places
for infection without the aid of wounds   The exposed cells often
have no protective cuticle and in addition are usually covered
with a sugary solution that is very favorable for germination of
fungus spores and growth of bacteria   Some nectary glands
are covered with an epidermis, the nectar exuding through
stomatal openings   In nectaries of this type, the nectar forms a
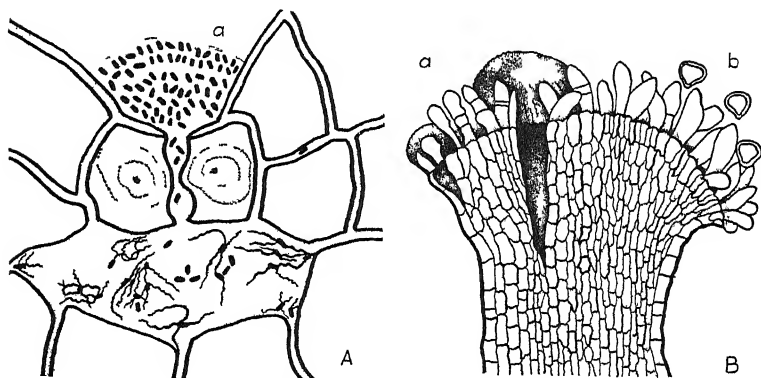
Fig 198 —Diagrammatic drawings showing methods of blossom infection by the
fire-blight bacteria, *A*, through a nectary stoma, *a*, bacteria in a drop of nectar
B, through a stigma, *a*, bacterial mass penetrating the intercellular spaces of
the stigmatic surface, *b*, pollen grains   (*After Hildebrand*)

continuous fluid connection from the exuded nectar drops into
the intercellular spaces (Fig 198)   Certain species of pathogenic
bacteria multiply rapidly in nectar and utilize the nectar glands
as avenues of entrance

Insects of many kinds visit flowers regularly in search of nectar
or pollen and in so doing often disseminate inoculum to the very
place where infection is most readily accomplished   As examples
of this may be mentioned fire (blossom) blight of orchard fruits
infecting through nectaries, stigmas, anthers, stomata, and
hydathodes and spread by bees, flies, and other insects, the anther
smut of pinks infecting through the stigmas and spread by the
sphinx moths, the seed blight of clover infecting through the
stigmas and spread by bumblebees, and ergot of grasses infecting

through the floral organs and spread by many different kinds of insect   All of these diseases are regularly transmitted by one or more species of insects that habitually visit both healthy and diseased flowers of susceptible plants in search of food, and the unprotected floral parts form the chief and often the sole avenue of entrance for the pathogens

The Periderm —In the stems of all plants having secondary growth, the epidermis is eventually replaced by another protective covering called the "periderm"   This is composed largely of cork cells and is even more effective than the epidermis in
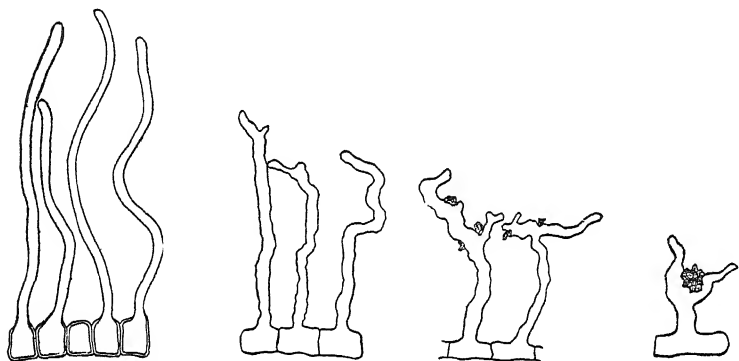
FIG 199 —Root hairs   These are specialized epidermal cells through which solutions are absorbed from the soil   They are short-lived, persisting for a few days only, after which they die   The adjacent cell walls quickly become suberized, preventing much infection from soil organisms   (*After Eames and MacDaniels*)

protecting the plant against infection by microorganisms   Cork cells are nonliving and possess walls that have been infiltrated with suberin, a substance similar in physical and chemical properties to cutin   The suberized cork cells are highly impervious to air and water   The periderm may cover the entire plant except the root tips and the buds, leaves, and flowers   It is the bark of woody plants and the corky covering of all roots   No bacteria and relatively few fungi are capable of penetrating, without aid, the unbroken periderm   However, this protection does not prevail against many insects, such as bark-inhabiting insects which are responsible for the ingress through the periderm of many destructive plant pathogens   *Ceratostomella ips*, the fungus causing blue stain of conifers transmitted by the pine bark beetles, and *C ulmi*, causing the Dutch elm disease transmitted

by the elm bark beetles, are good examples of pathogens that
gain ingress through the bark with the aid of insects

With the exception of the root tips and the short zone of absorp-
tion, covered with root hairs, the entire root system is protected
by a periderm of suberized cells   The root periderm is an effec
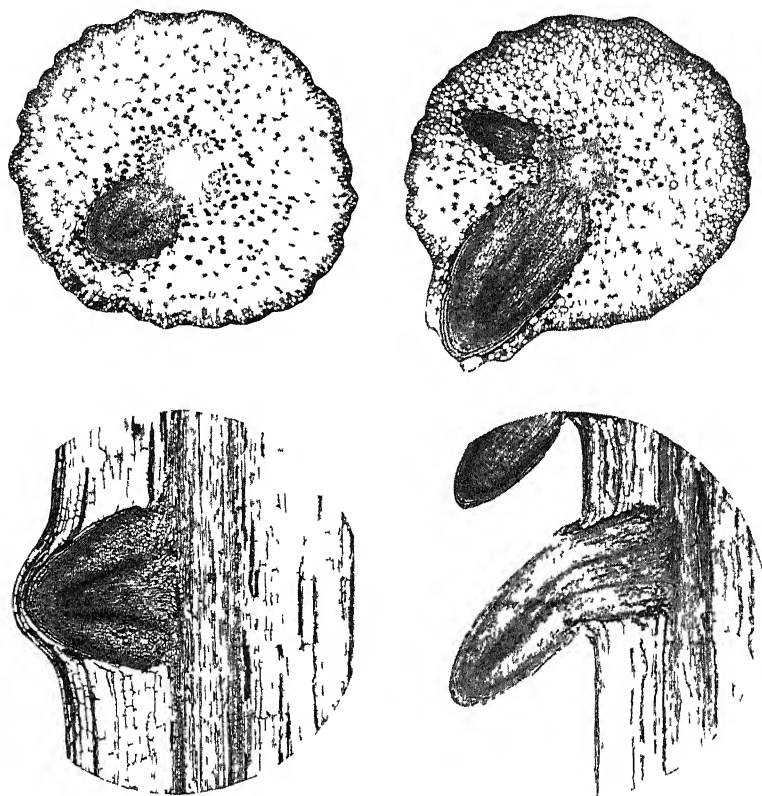
Fig 200 —Sections of a root of *Salix nigra* showing the endogenous origin
of secondary roots and the natural wounds made in the cortex   Such natural
wounds in certain plants serve as portals of entry for some soil-borne fungi
(*After Eames and MacDaniels*)

tive protection against many of the pathogenic organisms that
thrive in the soil   Yet despite this protection many pathogens
infect through some underground part of the plant   It is gen-
erally assumed that many of them enter through the root hairs
(Fig 199), which are not protected by a cuticle, but in many cases
the evidence is lacking   Natural wounds formed by secondary

roots (Fig 200) have been shown to serve as portals of entry for a few soil-borne fungi, but the extent to which these wounds are significant in root infection is not well known Because of the obvious difficulty of observing underground infection, the exact place and method of such infection is known for only a few pathogens Many insect pests of plants are known to spend all or part of their life history underground, and many of them feed on the roots of plants Where the root feeding is not excessive, it usually escapes observation Although a few cases of root infection through insect wounds have been well established, the extent to which insect wounds on roots serve as infection courts for plant pathogens is not known There is room for much study on the soil-inhabiting insects in relation to those diseases which infect through the underground parts of plants As examples of known root inoculation by insects may be mentioned crown gall, inoculated by white grubs and other soil insects, and the bacterial wilt of corn, inoculated by the southern corn root worm and the seed-corn maggot

Wound Cork —Cork tissue formed in response to a wound is known as wound cork Practically all plants are capable of forming cork tissue in the process of healing a wound The physiology of wound-cork formation has been extensively studied A good discussion of the subject is given by Priestly and Woffenden (1922, 1923) When plant tissue is wounded, those cells closest to the surface of the wound die within a few hours, but, in the process, the chemical and physical nature of the cell walls undergo a striking change The fatty acids in the cell sap are oxidized and are precipitated in and on the surface of the cell walls, making them relatively impervious to water This is the so-called "blocking" process that prevents the excessive loss of water, and it has been demonstrated that the blocking tissue is an effective barrier against infection by many pathogens After the blocking process is complete, the cells beneath this tissue become meristematic, forming a cork cambium the cells of which divide to give rise to new layers of cells which are quickly suberized and form a new periderm (Fig 201) An abundant supply of oxygen and a supply of reserve food materials are necessary for wound-cork formation The healing of wounds in this way constitutes one of the most effective natural protections of plants against infection There are certain insects, however, that burrow into

plant tissue and make wounds that are more or less continuous over a relatively long period of time   Such insects, by interfering with the healing process, overcome, to a considerable extent, the protective effect of wound-cork formation   The activity of the seed-corn maggot, in inoculating potato seed pieces with the bacteria that cause blackleg, is of this nature   The larvae of this insect burrow into the seed pieces, inoculate them with the soft-rot bacteria, and destroy the wound tissue as fast as it is formed
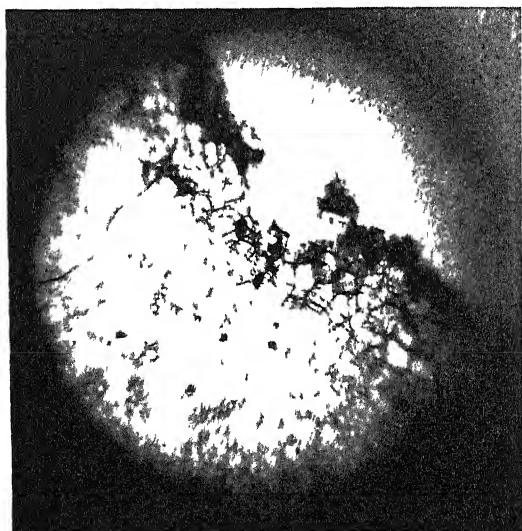
Fig 201 —A section through a healed wound in a potato tuber   Note the dark irregular-shaped cells that compose the blocking tissue and the layer of more regular brick-shaped cells making up the new wound periderm that has formed from a cork cambium

The continual wounding of the tissues by the maggots ensures successful infection by the bacteria

Callus —When a wound is of considerable size and involves the cambium, another kind of wound tissue known as "callus" is often formed   Callus is composed of soft parenchymatous tissue produced rapidly by the cambium (Fig 118)   The outer cells of the callus tissue differentiate and become suberized to form a protective bark   The continued growth of the callus tissue permits the healing of large wounds, such as those made in pruning when large limbs are cut off   Callus tissue, like wound cork, is a relatively effective barrier against infection by micro-

organisms, but its soft and succulent nature makes it an attractive food for certain insects   The insects, by acting as vectors of plant pathogens, often overcome the protective action of the callus and cause it to function as an infection court   This situation is well illustrated by the relationship of the woolly aphis to the perennial canker of apple trees, in which reinfection occurs each year through wounds made in the callus tissue by the aphids (McLarty 1933 and Childs 1929)   Delicate, blisterlike swellings are formed on the callus as a result of the aphid feeding   During the winter the blisters freeze and collapse, providing a suitable point of entrance for the spores of *Gleosporium perennans* which are ever present in the old cankers   Because the trees are dormant when this occurs, infection is accomplished and considerable tissue is destroyed before renewed growth of the callus can take place

Latex Ducts —With the discovery of plant-parasitic protozoa (Lafont 1911) which are confined almost entirely to laticiferous plants and are exclusively insect-transmitted, the latex ducts assumed a new significance in the study of plant diseases and their transmission by insects   As pointed out by Holmes (1925c), failure to understand the nature of latex ducts and the relation of the protozoa to them often leads to a misinterpretation of the facts

The latex ducts are living cells   They contain many nuclei and ramify for long distances through the tissues of the plant   The protoplasm contains large elongate vacuoles which are filled with the milky latex   The ducts have no opening to the outside of the plants, and the protozoa are therefore dependent upon insects for their introduction into the latex cells   The protozoa do not occur in the protoplasm but are found only in the latex of the vacuoles

There are two different kinds of latex duct, classified according to their mode of origin   One type, usually designated "latex cells," arises by the elongation of a single cell which grows and branches in the manner of a fungus mycelium   Each cell is a distinct unit, and the individual cells do not anastomose with one another

Another type of latex duct arises from many different cells that unite by dissolution of their adjacent end walls   These ducts are usually referred to as "latex vessels"   Latex vessels

are characteristic of such plants as lettuce and other laticiferous composites, whereas the latex cells are found in the euphorbias and milkweeds in which most of the endophytic protozoa are found   The two types of latex duct are represented in diagrammatic form in Fig 175

Physiology and Chemical Composition.—The activities of insect vectors are influenced not only by the anatomy of their host plants but also by their physiology   Considerable evidence is available to show that differences in chemical composition of different varieties of plant greatly influence the degree to which they are attacked by certain insects   Many species of plant possess qualities of insect resistance that are obviously based on physiological differences   In many cases, the direct injury caused by the insects may not be sufficiently great to make the differences in resistance obvious or of much economic importance, but if the insect happens to be a vector of a plant pathogen, its preference or dislike of a given variety may be of great significance in the epiphytology of the disease   This is especially true of the virus diseases and their insect vectors, although it applies equally well to all diseases of parasitic origin   Inspection, roguing, and certification of seed or plant parts have become standard procedures in the control of many virus diseases   The rapidity with which a virus spreads in nature often determines the success of certification as a control measure, and the rapidity of spread is often determined by the habits of the vector   Varieties that are preferred by a given insect vector would be more likely to contract the disease than those shunned by the insect, although the varieties may be equally susceptible to the virus when inoculated   Plants that escape infection for this or some similar reason, although they are susceptible to the disease when inoculated, are said to be "klendusic" (Rankin 1927)   Because of the significance of klendusity in the practical control of virus disease, this character is deserving of more attention than it has received   In the production of new varieties of crop plants, breeding for klendusity may be of as much practical importance as breeding for true resistance   If the disease is transmitted in nature by insects, breeding for klendusity may offer more promise than breeding for immunity, and tests of hybrid progenies should be made with this in mind   A more

careful study of insect relationships seems desirable in breeding for resistance to insect-transmitted diseases

Rankin (1927) was among the first to call attention to klendusity in relation to plant-disease control   He showed that certain varieties of red raspberry escaped infection under field conditions, although, when inoculated under controlled conditions, they were very susceptible   The rate of spread of mosaic in the field was also lower on the klendusic varieties than on the varieties preferred by the insect vectors

This relationship has been investigated further by Schwartze and Huber (1937), who demonstrated a striking difference in susceptibility of red-raspberry varieties to *Amphorophora rubi* Kalt , the vector of raspberry mosaic (see Table III)   These authors observed that the spread of mosaic appeared to be directly proportional to their relative aphid populations   The variety Lloyd George was shown to be so highly resistant that the aphids could not maintain themselves on it   In western Washington, this variety was never found infected with mosaic although graft inoculations demonstrated its susceptibility   In a later and more complete report, Huber and Schwartze

TABLE III.—FIELD COUNTS OF *Amphorophora rubi* KALT , MADE UPON TEN RED-RASPBERRY VARIETIES*

Variety	June 25		July 25	
	Range of aphid counts per cane	Av no aphids per cane	Range of aphid counts per cane	Av no aphids per cane
Antwerp	0–2	0 2	0–5	1 8
Chief	8–104	42 7	3–108	41 1
Cuthbert	0–16	5 0	0–30	10 8
Herbert	0–3	0 3	0–6	1 8
Latham	2–27	14 7	4–49	23 1
Lloyd George	0–0	0 0	0–0	0 0
Marlboro	1–9	4 6	4–42	16 8
Newburgh	0–6	2 0	0–9	4 6
Newman	4–17	10 1	1–26	12 5
Viking	0–39	16 0	3–83	32 8

* After Schwartze and Huber

(1938) added the varieties Indian Summer, Pyne Imperial, and Pyne Royal to those on which *A rubi* could not maintain its population   Reproduction was slow and the population remained small on Antwerp, Herbert, Marcy, and Newburgh

The nature of the resistance to the aphids was not determined, although it was stated that "the behavior of *Amphorophora rubi* when confined to Lloyd George plants under cages indicates that resistance probably results from a lack of suitable food for the insect rather than the presence of an actively repellent substance"   When the variety Lloyd George was crossed with susceptible varieties, the aphid-resistant character was inherited The significance of a knowledge of these relationships in the breeding of improved varieties of raspberries is obvious   A true mosaic-resistant variety would be desirable, but if this is not easily obtained, a klendusic variety would be of great economic value   Even though only partial control could be obtained by the use of such varieties, the efficiency of control of mosaic through certification would be greatly increased by the slower rate of spread of the disease on klendusic varieties

A similar relationship has been shown to exist among varieties of cranberry and the leaf hopper (*Euscelis striatulus*), vector of cranberry false blossom (Wilcox and Beckwith 1933)   The degree of susceptibility of cranberry varieties under field conditions and the relative rate of spread of the disease were shown to be directly correlated with their attractiveness to the leaf hopper

One of the best known examples of resistance to insect injury in plants is that of the native American grapes to the grape *Phylloxera* (*Phylloxera vastatrix* Planchon)   This insect is a native of Eastern North America and commonly infests the various species of wild grape that, through natural selection, have acquired a high degree of tolerance to the insect   When the *Phylloxera* was introduced into France about 1860, the European species of grape proved to be so susceptible that within 25 years nearly one-third of the vineyards of France had been destroyed by it   The *Phylloxera* attacks both leaves and roots, but the greatest injury is caused by those which feed upon the roots Numerous soft, watery galls are formed on the infested roots These galls soon decay and greatly impair the root system, and the death of the entire plant is often the result

Many control measures have been used in combating the *Phylloxera* on European grape varieties, but the most successful has been the use of certain species of American grape as resistant stocks on which to graft the desired European species The mechanism of the resistance or tolerance of the American varieties is not known

Searls (1935) has shown that varieties of peas with normal yellow foliage are more resistant to the pea aphid [*Illinois pisi* (Kalt)] than those varieties with darker green foliage It is not known whether the reaction is caused by the color alone or by some other factor associated with it Because the aphids are the most common vectors of virus diseases, this discovery is obviously significant in the study of insects in relation to the transmission of virus diseases in general It will be very interesting to know if other aphids react in a similar way to the color of the host plants

An extensive study of the resistance of sorghums to the chinch bug has been reported by Snelling, Painter, Parker, and Osborn (1937) A wide variation in resistance was found, and the inheritance of the character was demonstrated Resistance is due, not to a preference for the more susceptible varieties, but rather to the ability of the plant to grow or recover regardless of the continued feeding of the chinch bugs The exact mechanism of resistance was not determined These authors give a comprehensive review of the literature on insect resistance in plants

The problem of inherent plant resistance to insects has been discussed at some length by Folsom and Wardle (1934), who cite numerous references bearing on the subject, and by Sweetman (1936) The latter, in considering the causes of resistance, groups them into three categories as follows

1 Physical factors, such as thickness of epidermis and degree of pubescence

2 Chemical factors, the presence in the plant of alkaloids, acids, tannins, or other chemicals

3 Physiological factors, including vigor, quick recovery from injury, seasonal adaptation, early maturity, and copious sap flow

Sweetman lists 66 examples of plant resistance to insects involving 47 different species or varieties of plant, and a some-

what larger number of insects   Of these, 17 were classed as caused by physiological factors, 10 by physical factors, 9 by chemical factors, and 8 by both physical and chemical factors, and 22 were classed as unknown

The problem and its practical possibilities have been neglected somewhat by entomologists, as pointed out by Mumford (1931), who has discussed briefly some of the factors involved in insect resistance   He has proposed two new terms to express his concept of the nature of the resistance   Insect resistance caused by external protective agencies such as a thick epidermis or excessive pubescence is called *epiphylaxis*   Resistance caused by internal factors such as the nature of the cell sap or protoplasm is called *endophylaxis*   The latter category would include not only those characters that are unattractive or repellent but also the failure of the cell contents to meet the food requirements of the insect

A very good discussion of the resistance of plants to insect injury was presented in 1924 by McColloch, who stressed the need for a more fundamental study of the subject   Less extensive general discussions of the subject of plant resistance to insect attack have been published by Ticheine (1917), Lees (1926), Parker and Painter (1932), McLeod (1933), and others McColloch recognized six kinds of specific cause of resistance (1) habit of growth, (2) morphological characters of plants, (3) physiological characters of plants, (4) mechanical factors, (5) ability to recover from injury, and (6) external or environmental factors

Insect resistance often escapes observation because the insect itself is not noticeably injurious, but it should be remembered that insect vectors of plant diseases may be very destructive indirectly through the diseases that they transmit   The inherent resistance of plants to insect vectors, therefore, should not be overlooked in the study of plant diseases transmitted by insects

The demonstration by DeLong, Reid, and Dailey (1930*a*, *b*) that bean plants sprayed with Bordeaux mixture may absorb enough copper to kill leaf hoppers feeding upon them calls attention to a new type of artificially induced insect resistance in plants   There has not been sufficient investigation of the possibility of this method of insect control to justify generalizations as to the extent of its application in the control of plant

diseases through control of insect vectors It has possibilities
enough to justify more extensive investigations

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CHAPTER XIII

THE ANATOMY AND PHYSIOLOGY OF INSECTS IN RELATION TO THE TRANSMISSION OF PLANT DISEASES

The complexity of the relationship between insect vectors and the disease that they transmit varies widely   The association may be a simple, mechanical one or may involve a highly developed state of symbiosis   Even in the less complicated relationships, the association is often based on some particular adaptation in the morphology or physiology of the insect vector   It is evident that some knowledge of insect anatomy and physiology is essential for a satisfactory understanding of the nature of insect transmission of plant diseases   Certain aspects that are of particular significance in a study of insect transmission of plant diseases will be discussed briefly in this chapter   Emphasis will be placed on the anatomy and physiology of those orders of insect which include species of recognized importance as vectors   For a more complete treatment of insect anatomy and physiology, the reader is referred to the work of Snodgrass (1935), Comstock (1936), Imms (1934), and Weber (1930) and to the numerous other standard entomological texts

THE EXOSKELETON

Insects are small boneless animals possessing a sclerotized exoskeleton instead of the bony endoskeleton of the higher animals   The exoskeleton protects the more delicate internal structures from desiccation and from mechanical injury, and it serves also as a very satisfactory framework for the attachment of muscles   The exoskeleton is made up of three essential layers   One layer of living cells, the *epidermis*, is covered externally with a nonliving and noncellular layer, the *cuticula*, and is bounded internally by a very thin layer of noncellular structure, known as the *basement membrane* (Fig 202)   The cuticula is a secretory product of the epidermis and consists chiefly of a nitrogenous polysaccharide known as *chitin*   It is soft at

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fiist but becomes hard and tough by infiltiation with a veiy
iesistant scleiotizing substance   The cuticula is composed of
two layers, the outer, heavily scleiotized *exocuticula* and the
innei, thickei, laminated *endocuticula*   A veiy thin suiface
layei known as the *epicuticula* is often present   The cuticula
may be smooth and glistening or variously sculptured by stiia-
tions, granulations, or other markings
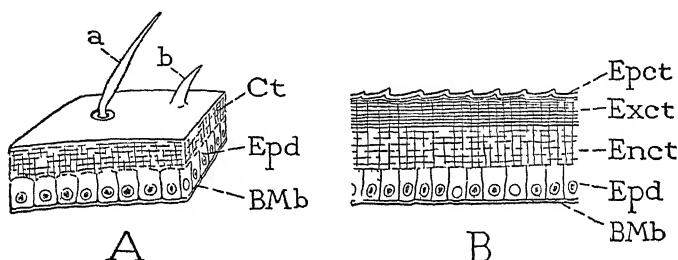
FIG 202 —A diagiammatic iepresentation of the stiuctuie of the body wall
of an insect   A, a thiee-dimensional view of a section of the body wall beaiing i
seta (*a*) and a fixed haii (*b*), B, a veitical section, *Ct*, cuticula, *Epd*, epideimis,
BMb, Basement membrane, *Epct*, epicuticula, *Exct*, exocuticula, *Enct*, endo-
cuticula   (*After Snodgrass*)

When the exoskeleton is concerned in the dissemination of
plant pathogens, the process is geneially of a mechanical nature
Dry spores, as well as wet sticky ones, adheie readily to the
exoskeleton of insects, and they aie likewise easily dislodged
Many kinds of fungus spore are disseminated mechanically in
this way by insects that visit diseased and healthy plants   The
effective surface for such mechanical dissemination of inoculum
is gieatly increased by the nature and abundance of cuticulai
processes   There are two general kinds of cuticular piocess
(1) The *setae*, or hollow pointed haiis, each pioduced by a modi-
fied epideimal cell, the *trichogen*   The setae usually have a
membraneous articulation at the base and a wide vaiiety of
shapes, structures, and functions   (2) The *miciotrichia*, oi
fixed hairs, consisting of very small pointed extensions of the
cuticula   These are fixed and solid and have no membraneous
articulation   They assume many shapes and sizes and are often
very numerous   All these cuticular processes and the body
appendages, such as legs, wings, and antennae, may serve as
structures that catch and distribute spores and other kinds of
inoculum (see Figs 22 and 220)   Inoculum that adheres to the

exoskeleton may be transported for long distances but usually, sooner or later, will be brushed off, either by accident or purposely by the insects Many insects are clean in their habits and frequently rid their bodies of adhering particles by means of their legs

THE MOUTH PARTS

Because feeding wounds made by insects are so important in disease transmission, the nature of the mouth parts assumes great significance in the study of insect structure from this point of view Moreover, there is greater variation in the form of the mouth parts than in that of almost any other portion of the insect's anatomy The variation in form is usually accompanied by a change in method of feeding These differences in mouth parts and feeding methods have much to do with the relative effectiveness of different insects in transmitting plant diseases Therefore, a knowledge of the different kinds of insect mouth parts is essential in a study of this kind

Notwithstanding the great variation in structure, the mouth parts of most insects fall into one of two general types (1) the mandibulate, or chewing mouth parts, and (2) the suctorial mouth parts adapted for piercing and sucking There are, however, many modifications involving intergradations and overlapping of these two general types so that further division is desirable We therefore recognize the following six types based on the methods of feeding (1) chewing, (2) rasping-sucking, (3) piercing-sucking, (4) sponging, (5) siphoning, and (6) chewing-lapping

The typical mouth parts of an insect consist of eight essential structures the *labrum*, the *epipharynx*, a pair of *mandibles*, a pair of *maxillae*, the *hypopharynx*, and the *labium* (Fig 203) These eight mouth parts vary so much in both form and function in different insects that they are often scarcely recognizable, but careful studies of their development and evolution have established their homologous nature

1 Chewing Mouth Parts —The chewing mouth parts are adapted for pinching off, chewing up, and swallowing bits of tissue They are well illustrated by the mouth parts of a grasshopper (Fig 203) The *labrum*, or the so-called "upper lip," fits over the mandibles in front and helps to pull the food into

the mouth   The *epipharynx* is a structure forming the ventral surface of the labium and is continuous with the roof of the mouth and esophagus   Usually, it is equipped with organs of taste   The *mandibles*, or first pair of jaws, often called "teeth," are the structures that bite off and masticate the tissues   They

Labrum

Epipharynx   Hypopharynx

Right mandible   Left mandible

Labium

Right maxilla   Left maxilla
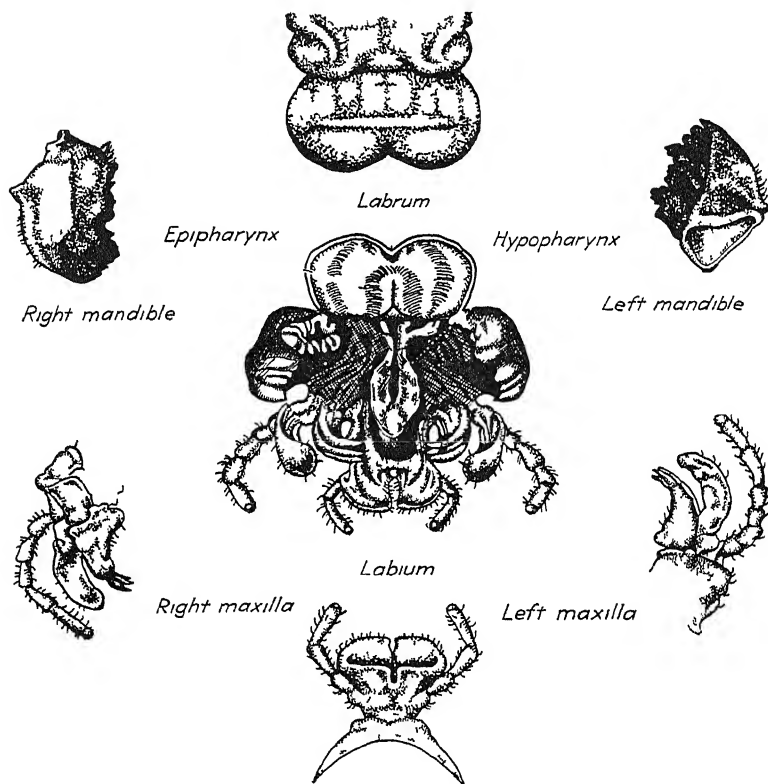
Fig 203 —The mouth of a grasshopper, a typical chewing insect, showing the various parts   These fundamental structures are modified in the different species of insects to form mouth parts of widely different forms and functions (*Redrawn from Metcalf and Flint*)

are hard and usually equipped with sharp, pointed projections that make them effective grinders   Their chewing action is from side to side   The *maxillae*, or second pair of jaws, are more complicated in structure than the mandibles, each being composed of several articulated units (*cardo, stipes, palps, palpifer, galea,* and *lacinia*)   Some of these work from side to side much

like the mandibles and aid in chewing Others are antennaelike and are sense organs The *hypopharynx* is a tonguelike prolongation of the floor of the mouth and is attached to the inside wall of the labium The opening of the salivary duct is usually closely associated with the hypopharynx The *labium*, or lower lip, is found opposite the labrum, or upper lip It is composed of a third pair of jaws or appendages grown together along the mid-line and forming a lower lip It has a pair of short antennaelike appendages, or labial palps, that also serve as sensory organs

As representative of insects and chewing mouth parts may be mentioned grasshoppers, crickets, termites, and beetles Many larvae, especially those of the Coleoptera and Lepidoptera, also have chewing mouth parts These are the so-called grubs and caterpillars among which are found several important vectors of plant diseases

2 **Rasping-sucking Mouth Parts** —This type is intermediate between the chewing type and the piercing-sucking type and is represented by the mouth parts of thrips Thrips feed upon growing plants and are known to be vectors of several destructive diseases The mouth parts of various species of thrips have been studied by Borden (1915), Peterson (1915), Reyne (1927), and Wardle and Simpson (1927) The latter authors have described in considerable detail the mouth parts of *Thrips tabaci* Lind and also its method of feeding on the tissues of the cotton plant

The mouth parts of this insect are bent backward and underneath the head, forming a short cone-shaped proboscis (Fig 204) The front part of the cone is made up of the *clypeus* and the *labrum*, separated slightly by a membrane These structures are not symmetrical The sides of the cone are formed by triangular structures probably derived from the *maxillae*, each bearing a three-jointed palp The triangular *labium* composes the rear wall of the cone It is longer than the labium and maxillae and projects as a flexible flap Both the labium and the maxillae are equipped with small hooks that probably serve to grip the leaf surface

Four stylets enclosed within the cone are the actual piercing organs The stylets are not symmetrical, there being two paired stylets, one on each side of a median stylet, and a single unpaired stylet to the left The homologies of the stylets are

debatable, but, according to one interpretation, the paired stylets are probably of maxillary origin, the median stylet being derived from the *hypopharynx* and the left stylet being a *mandible*

According to Wardle and Simpson (1927), the insect in feeding on a leaf surface, gashes an epidermal cell with a pickax-like movement of the single mandible   Further destruction of the
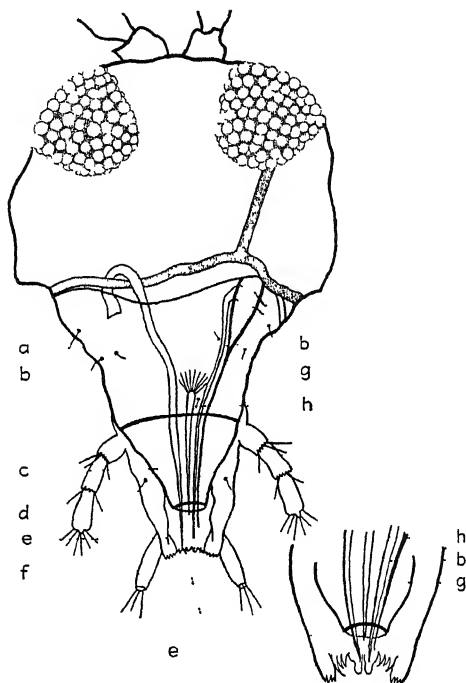
Fig 204 —The assymetrical mouth parts of *Thrips tabaci*   a, clypeus, b, maxilla, c, labium, d, maxillary palp, e, labium, f, labial palp, g, mandible, h, hypopharynx   (*Redrawn after Wardle and Simpson*)

underlying tissue is accomplished by the more delicate, paired, maxillary stylets which can penetrate deeper into the tissues than the mandible can   The contents of the lacerated cells are sucked into the pharynx by applying the mouth of the cone to the leaf surface   The head and mouth parts of one of these insects in the act of feeding on the surface of a leaf is shown diagrammatically in Fig 205

Another type of the rasping-sucking mouth parts is found in the muscoid larvae (maggots) of the Diptera   The usual

structures are entirely suppressed in the maggots, being replaced by a pair of strong, sharp, chitinous "mouth hooks," movable as a unit in a vertical plane   These mouth hooks are often incorrectly called mandibles   They are solid cuticular structures that are shed with each molt but are in no way homologous with true mandibles   The entire facial region of the head is invaginated into the thorax, and a fold of the neck projects
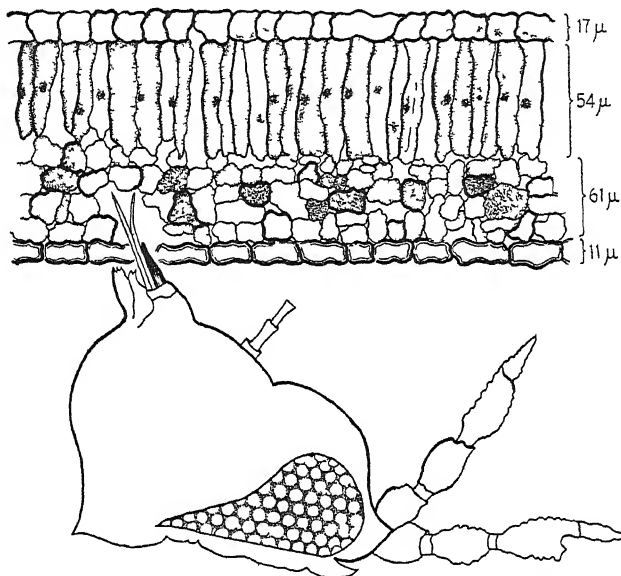
FIG 205 —A diagram of the head of a feeding thrips indicating its size in relation to the leaf tissues and the depth of the feeding wounds   (*After Wardle and Simpson*)

beyond the mouth to form a snoutlike structure that functions as the "head" of the maggot

In feeding, the maggot lacerates the plant tissues or other substrate with the mouth hooks and, by means of a pump, sucks in the released liquid food   This more or less continuous rasping action of maggots that feed on plant tissues constitutes a very effective wounding agency from the standpoint of infection by plant pathogens   The symbiotic association of maggots with bacteria and other microorganisms that often are pathogenic to plants makes them assume a role of particular significance in this respect

3 Piercing-sucking Mouth Parts—The mouth parts of those insects which feed by piercing and sucking are highly specialized, and it is difficult to recognize the component parts as homologous with those of the chewing insects There are many variations as represented by the aphids and plant bugs, the lice, the biting flies, and fleas We are primarily interested in the Homoptera and Hemiptera as plant vectors, and our discussion of the piercing-sucking mouth parts will be limited to representatives of these groups

The essential structures of the Hemipterous mouth parts are represented in Fig 206 They consist of a slender beak of three or four segments surrounding and partly enclosing four extremely slender, sharp-pointed stylets so fitted together as to resemble a single bristle These piercing stylets are often referred to as "mandibular" and "maxillary bristles" or merely as "setae" Since the latter term has been used extensively by those who have studied the mechanism of feeding of piercing-sucking insects on plant tissues, it is used in most of the following discussions

The beak enclosing the setae is not a complete cylinder but has a groove along one side in which the four setae lie This grooved structure is the *labium* The four setae are *mandibles* and *maxillae*, the latter being the innermost two enclosed by the pair of mandibles The inner surface of each of the maxillae is doubly grooved from end to end so that fitting together they form two closed tubes (Fig 206.1) The dorsal tube, usually the larger of the two, is the suction tube through which the plant juices are sucked The smaller, ventral tube is the salivary tube through which saliva is ejected into the plant

The two mandibles fit closely on opposite sides of the maxillae almost completely enclosing them but permitting a free sliding movement of the maxillae inside the enclosing mandibles Near the base of the labium, on the open, or dorsal, side, the groove is covered by a short flap, the labrum The hypopharynx lies between the bases of the maxillae It is penetrated by salivary ducts that open into the salivary tube It is heavily sclerotized but is small and inconspicuous

The structure as described above may be considered as representative of the plant-sap-sucking insects of the orders Homoptera and Hemiptera There is considerable variation in the details of structure among the different species of these orders,
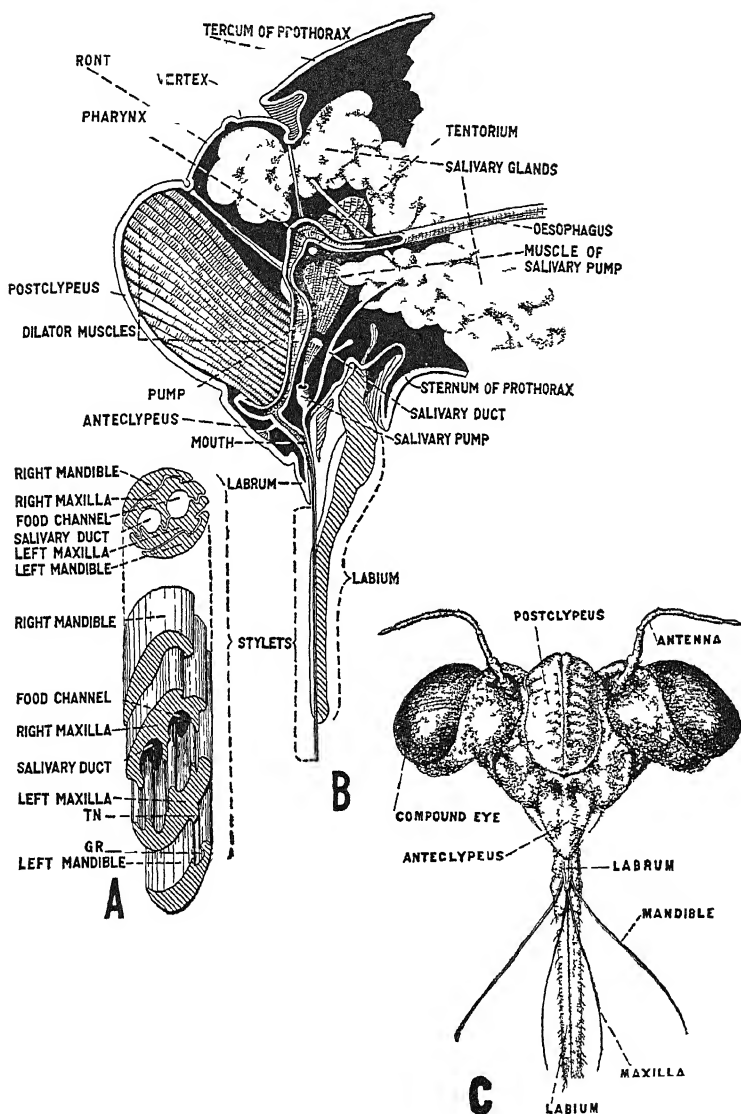
FIG 206 —The piercing sucking mouth parts of the squash bug and cicada
A, cross section and isometric projection of mouth parts of the squash bug, *B*, a
saggital section of the head of the periodical cicada showing the mouth opening,
the sucking pharynx, and the salivary glands, *C*, front or dorsal view of head and
mouth parts of a dog-day cicada   (*After Metcalf and Flint*)

but the fundamental arrangement of the mouth parts and their functions are essentially the same in all

The detailed mechanics of feeding by the piercing-sucking insects has not been studied very extensively   The small size of the insects and the nature of their feeding have made the subject a difficult one   In relatively recent years, since the importance of sucking insects as vectors of plant viruses has been fully realized, the subject has received renewed attention   Earlier descriptions were brief and vague   It was stated simply that the slender stylets, using the grooved labium as a guide, were forced into the plant tissue by the protractor muscles at their base   However, when the feeding punctures (Figs   223
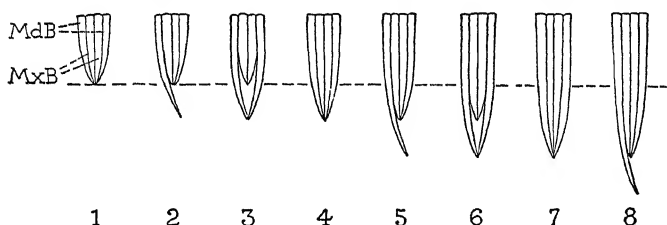
FIG 207 —Successive stages in the insertion of the set e of Hemiptera according to Weber's interpretation   *MdB*, mandibula set e, *MxB*, maxillary setae (*After Snodgrass*)

and 224) are examined, it is evident that the range of action of the protractor muscles is not sufficient to force the setae to the depth that they reach in the plant tissues   Moreover, in many species (*Psyllidae, Coccidae*, etc) the setae are much longer than the labium, and when the insect is not feeding the setae are retracted in a long flexible loop outside the labial groove   It would be physically impossible for the retractor muscles to force such long flexible setae into the plant tissues   The retraction of these long setae from the plant tissues would be difficult to explain, but Heriot (1934) has called attention to the fact, often overlooked, that the setae are cast off and renewed with each molt and that insects with very long setae, such as the scales and certain aphids, often never retract their setae after they once have been inserted deep into the tissues

The mechanics of penetration by these insects has been investigated more extensively by Weber (1933), who has shown that the four setae are not moved simultaneously as a unit by the protractor muscles but are moved independently of each other

According to this authority, the mandibular setae are the actual piercing organs and operate as follows One mandibular bristle is forced out in advance of the remaining setae for a short distance by the protractor muscles, the sharp point of the single bristle making a small opening in the plant tissue   This operation is followed by a similar thrust by the opposite mandible after which the two enclosed maxillary bristles are lowered so that all four bristles assume the original position relative to one another but are slightly embedded in the surface of the plant tissue   By continued repetition of this procedure, which is
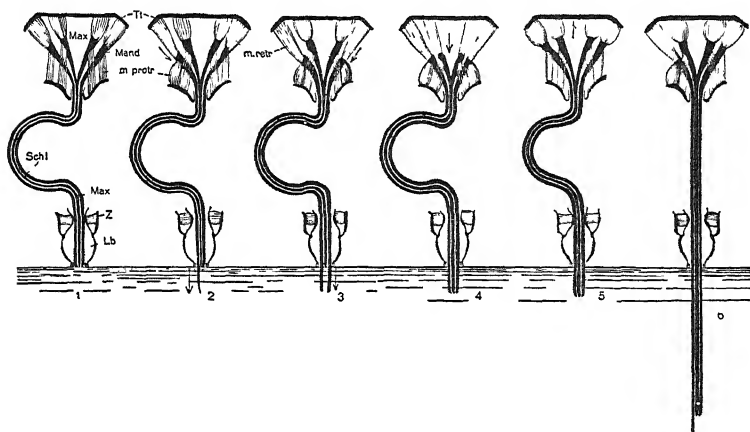
Fig 208 — A diagrammatic drawing illustrating the mechanism of penetration of plant tissue by Hemipterous insects having long setae stored in a coil when retracted   1, position of beak before penetration, 2 to 6, successive stages of insertion   (*From Snodgrass after Weber*)

illustrated diagrammatically in Figs 207 and 208, the setae are gradually driven deeper and deeper into the tissue until the required depth is reached   They are prevented from slipping back after each individual thrust, in some species by barbs on the mandibular setae and in others by the clasping action of the enclosing labium   According to Grove (1919), this clasping action may be due to increased pressure of body fluids, but Weber has shown that usually there are special labial clamps, equipped with appropriate muscles, for this purpose (Fig 208)

There is considerable variation in the structure of the mouth parts of the different families of the Hemiptera, and further studies may reveal variations from the mechanisms described above, but, in any case, the piercing-sucking insects are capable

of penetrating plant tissues with a surprising degree of skill and
are able to select the tissues most suited to their needs   For a
further discussion of the feeding of the sucking insects from the
standpoint of the plant tissues, see Chap XV

The sucking process begins as soon as penetration of the tissue
has been accomplished   This involves a flow of saliva outward
through the salivary canal into the tissues and a flow of the plant
juices inward through the food canal   The saliva is forced
through the salivary canal by the salivary pump, a muscular sac
connecting with the salivary duct   The force required for the
flow of the plant sap is provided, in part by capillarity and posi-
tive sap pressure in the plant, and in part by active suction
produced by the dilation of the pharynx   Thus, a two-way flow
through the beak is maintained during the feeding process an
outward flow of saliva and an inward flow of a mixture of plant
sap and saliva

The sucking insects are perhaps the most important group of
insect vectors of plant diseases   The nature of their mouth
parts and their mode of feeding make them effective agents of
inoculation and ingression   They are especially effective in the
transmission of virus diseases, and there appears to be a high
degree of adaptation to virus transmission in many species of
the Homoptera

4 Sponging Mouth Parts —This type is found in the common
housefly and other nonbloodsucking Muscidae as well as in
certain other families of the Diptera   In these, the *labium* is
modified into a fleshy, elbowed, and retractile proboscis, the end
of which consists of a pair of large spongelike organs, the *labella*
(Fig 209)   These are traversed by a series of tubular channels,
the *pseudotracheae,* opening by a narrow slit along the exposed
side   The food channel is formed by the labium, epipharynx,
and hypopharynx   The mandibles are lacking, and the maxillae
are modified into a pair of maxillary palps   Most insects with
mouth parts of this type are unable to penetrate either plant
or animal tissue, but there are some species in which the cleft
between the labellar lobes is armed with several rows of small,
sharp *prestomal teeth* with which tissue may be injured by a
rasping action   The skins of animals are often lacerated by
insects equipped with prestomal teeth, but the mechanism is not
known to be used by any plant-feeding species

When feeding on liquid matter, the pseudotracheae are brought into contact with the liquid and are filled by capillary action The pseudotracheae all converge at a single point near the mouth of the food channel, and from this point the liquid is sucked into the esophagus   In feeding on solid material the labellum is placed on the food, and the liquid contents of the crop are regurgitated along with salivary secretions   This liquid dissolves the solid material and is again sucked in with the newly dissolved food

This habit of regurgitation is of considerable significance in the dissemination of pathogenic microorganisms   It has been shown
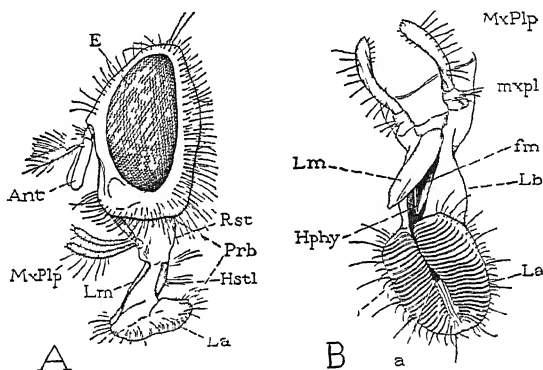
Fig 209 —Head and mouth parts of the common housefly (*Musca domestica*) *A*, lateral view of head with proboscis extended, *B*, anterodistal view of proboscis showing the pseudotracheae (*b*) leading to the aperture (*a*) which leads to the food channel (*fm*) that lies between the labium and the hypopharynx   (*After Snodgrass*)

that the liquid contents of the crop of certain species of fly contain large quantities of viable bacteria among which pathogenic species are frequently found   It would be difficult to conceive of a more effective method of distribution of these microorganisms by insects than the one provided by this method of feeding, and there is considerable evidence that insects of this type are important vectors of several plant diseases

5 Siphoning Mouth Parts —The mouth parts of moths and butterflies are of the siphoning type   Only in rare cases are they able to penetrate plant or animal tissue   Such mouth parts are highly specialized for feeding on liquid food (Fig 210)   The labium and the mandibles are usually absent or very greatly reduced, and the labium occurs only as labial palps   The

proboscis is formed by the two maxillae, the galeae of which are greatly elongated, each with a channel along its inner surface The two grooved galeae are held together by hooks and interlocking spines, forming a long tubular proboscis through which
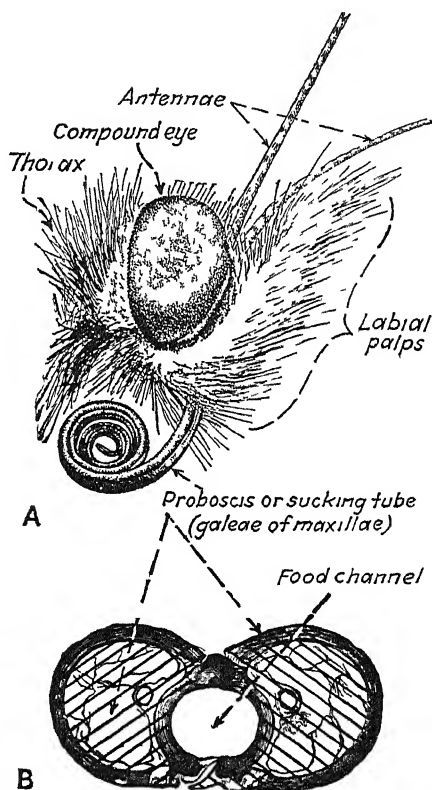
FIG 210 —The siphoning mouth parts of a moth or butterfly   A, a side view of the head with proboscis partly coiled, B, a cross section of the proboscis showing the right and left galeae locked together to form a food channel   Insects with siphoning mouth parts do not make wounds in plant tissue but may act as vectors for plant pathogens that infect through the floral organs   (*After Metcalf and Flint*)

liquid foods are imbibed   When not in use, the proboscis is coiled up like a watch spring   In feeding, it is uncoiled, and the tip is inserted into a liquid food such as the nectar of flowers The siphoning mouth parts are characteristic of adult Lepidopterous insects (moths and butterflies)   The larvae of these insects

(caterpillars), however, usually have mandibulate mouth parts adapted to chewing

Insects with siphoning mouth parts act as vectors of plant diseases chiefly as a result of their regular visits to flowers in
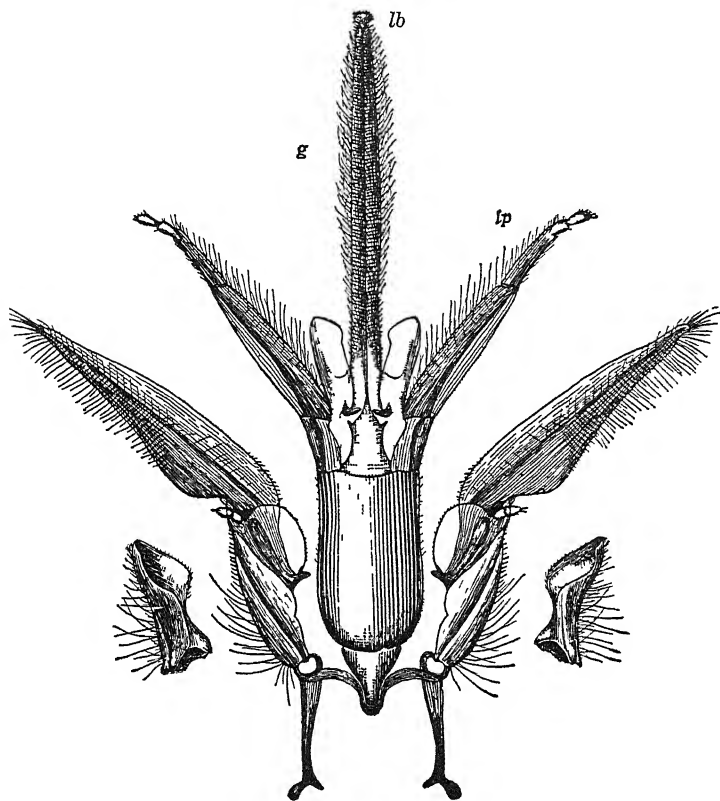
FIG 211 —The mouth parts of the honeybee   Ventral aspect showing the grooved glossa (*g*) with the terminal spoonlike labellum (*lb*)   In feeding position, the labial palpae (*lp*) cover the grooved glossae, forming a suction tube through which the nectar passes   The labellum serves as a spoon to lap the nectar from relatively inaccessible places   (*After Folsom and Wardle*)

search of nectar   The pathogens disseminated are those which find the flowers a favorable place for infection, and the inoculum is disseminated mechanically without wounding in all the known cases   The inoculum usually adheres to the setae or other bristlelike processes that serve also for the transfer of pollen grains

6. Chewing-lapping Mouth Parts —The honeybee and certain other species of Hymenopterous insects have complicated mouth parts representing a combination of the chewing type and a lapping tonguelike structure (Fig 211) The labium and mandibles are of the chewing type but are used more as tools in processing food than in feeding The labium, however, has been modified to form a lapping tonguelike proboscis, the *glossa* This structure is deeply grooved and densely covered with hairs except at its base, terminating in a small spoonlike lobe, the *labellum* There seems to be a difference of opinion as to how these structures are used in feeding, probably, they are used in different ways Easily accessible liquid foods are sucked into the mouth through a temporary food channel formed by the glossal tongue of the labium and the two labial palps If the food is less accessible, suction is aided by a rapid lapping movement of the glossal tongue In any case, the insects with mouth parts of the type represented by the bees, like those with siphoning mouth parts, are concerned chiefly with mechanical dissemination of inoculum that infects the floral organs They make no wounds in the plants that are of importance in infection Certain other Hymenopterous insects, such as the sawflies, have mandibles adapted for chewing and make wounds of various types on plant tissue This is especially true of many of the Hymenopterous larvae

THE SALIVARY GLANDS

Practically all insects are equipped with a pair of salivary glands generally located in the thorax, one on either side of the fore-intestine (Fig 206*b*) The ducts from the two glands unite to form a common salivary duct with an opening between the labium and the base of the hypopharynx There is often a saclike salivary reservoir opening off the salivary duct

Relatively little is known about the exact functions of the salivary secretions, but they are known to vary considerably in the different kinds of insect Their close association with the mouth parts obviously indicates that they are concerned in some way with the act of feeding In the case of a number of plant-sap-sucking insects, it has been shown that the saliva possesses diastatic action, converting starch into soluble sugars There is some evidence that the saliva has a solvent action, also, on

other cell constituents   Since the food canal is extremely small, often less than 1 or 2 microns in diameter, a low viscosity of the sap and the absence of occluding particles would be decidedly advantageous   In many sucking insects, a so-called "setal sheath" is formed around the embedded setae   This is thought by some to be largely of salivary origin and by its nature seals the opening, making it airtight, and increases the efficiency of the sucking operation

The salivary glands appear to be in some way associated with the biological transmission of plant viruses by insects, but the exact nature of the association is not clearly understood   Inasmuch as the mouth parts of the piercing-sucking insects do not permit of the regurgitation of ingested plant sap, the virus particles ingested with the sap apparently find their way through the insect's body, accumulate in the salivary glands and are transmitted to healthy plants in the salivary secretions

The salivary secretions of many insects are distinctly toxic to plant tissues, whereas those of other species apparently are harmless   The nature of the toxicity is not known, but it expresses itself in a variety of ways   A relatively large group of pathological effects, involving local injury or general physiological disturbances, is caused by insects that inject their salivary secretions into the plants   For a more complete discussion of this aspect of the problem, see Chap V

THE ALIMENTARY CANAL

The alimentary tract of the vector is involved to some extent in practically all cases of insect transmission of plant diseases, except in those consisting of simple mechanical distribution of inoculum   When transmission is biological, there is often a symbiotic relationship in which the alimentary canal and its appendages are structures of vital importance   Striking anatomical modifications of the digestive tract often occur as a result of symbiosis with microorganisms   A knowledge of the structure and function of this organ, therefore, would appear to be necessary for fundamental study of insect transmission of diseases   Insects of many different species regularly ingest quantities of inoculum of plant pathogens   Relatively little is known of the fate of the ingested inoculum and its significance in the spread of the disease concerned   In the following pages,

a brief description of the digestive system of insects will be given, with particular reference to those structures and functions which are potentially of significance in disease transmission

The alimentary canal of insects is essentially a tube   It may be straight, or variously looped if its length exceeds that of the body   It is functionally a device for holding food in close contact with digestive and absorptive surfaces, having at one end a special organ of ingestion and at the other an organ of egestion   The digestive canal is composed of three primary divisions (1) the *stomodaeum*, or fore-intestine, (2) the *mesenteron* (*ventriculus*), or mid-intestine, and (3) the *proctodaeum*, or hind-
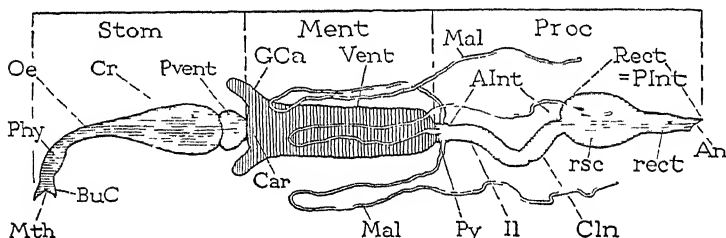
Fig 212 —A diagrammatic and conventionalized alimentary canal of an insect showing the usual subdivisions and typical outgrowths   *Stom*, stomodaeum, *Mth*, mouth, *BuC*, buccal cavity, *Phy*, pharynx, *Cr*, crop, *Pvent*, proventriculus   *Ment*, mesenteron, *GCa*, gastric caecum, *Car*, cardiac valve, *Vent*, ventriculus, *Proc*, proctodaeum, *Mal*, Malpighian tubules, *Py*, pyloric valve, *AInt*, anterior intestine, *Il*, ileum, *Cln*, colon, *Rect = PInt*, posterior intestine or rectum, *An*, anus   (*After Snodgrass*)

intestine   These divisions are usually separated by valvelike structures, the one separating the stomodaeum from the mesenteron being known as the *stomodael*, or *cardiac* valve, and the one between the mesenteron and the proctodaeum, the *procto-daeal*, or *pyloric* valve (Fig 212)

1 The Stomodaeum —The stomodaeum, or fore-intestine, is of ectodermal origin and is formed in the embryo as an invagination from the outside   The stomodaeum, therefore, is lined with cuticula of the same origin as that of the exoskeleton   This cuticular lining is cast out and renewed each time the insect molts, a fact of considerable significance in a study of the possible survival of microorganisms in the insect body during metamorphosis

In its simplest form, the stomodaeum is little more than a tube connecting the mouth with the mesenteron, but in most insects

it has become differentiated into three regions, the *pharynx*, the *crop*, and the *proventriculus* In addition, an undifferentiated section between the pharynx and the crop may serve as an esophagus In some insects, the section just within the mouth proper is distinguished from the mouth as the *buccal cavity* The primary functions of the stomodaeum are largely mechanical, but some digestion often takes place in the crop where the food is subjected to the salivary enzymes as well as to gastric juices that flow forward from the mesenteron

The *buccal cavity* is the oral part of the stomodaeum and usually is not differentiated sharply from the pharynx In ants, there is a well differentiated *infrabuccal chamber* in the form of a spheroidal sac opening into the mouth cavity by a short constricted canal (Fig 35) This chamber is used as a repository for any solid material ingested by the ant with its liquid food The accumulated residue is thrown out as a compact pellet It has been shown by Bailey (1920) and Leach and Dosdall (1938) that these infrabuccal pellets often contain viable fungus spores and that ants are by this means potential vectors of plant diseases The infrabuccal chamber is used also by the fungus-cultivating ants for transporting cultures of the fungus when new colonies are established

The *pharynx* lies just behind the buccal cavity, with strong dilator muscles attached to its walls In insects with piercing-sucking mouth parts, the pharynx is a highly developed pump, or sucking device, by means of which the liquid food materials are ingested

The *esophagus* is merely a narrow section of the stomodaeum between the pharynx and the crop It has no function other than the conduction of food to the crop

The *crop* may consist of a simple enlargement of the posterior region of the esophagus, but in some insects it occurs as a lateral diverticulum of the esophagus The diverticulum usually forms a simple sac, but in the Diptera it takes the form of a long slender tube with a bladderlike enlargement at the end (Fig 213) The primary function of the crop is that of food storage Most insects feed excessively when food is available, storing the excess food in the crop to be passed later into the ventriculus for digestion There is evidence, however, that some digestion also takes place in the crop through the agency of salivary enzymes and

digestive fluids that flow forward into the crop from the ventriculus   There is no conclusive evidence that enzymes are secreted by the walls of the stomodaeum or that an appreciable amount of absorption takes place through them

The contents of the crop of the Diptera are usually liquid and contain large numbers of bacteria and other microorganisms that play a part in the digestion of the food   This is regurgitated along with salivary secretions when the insect is feeding on solid or semisolid material   The regurgitated liquids dissolve the
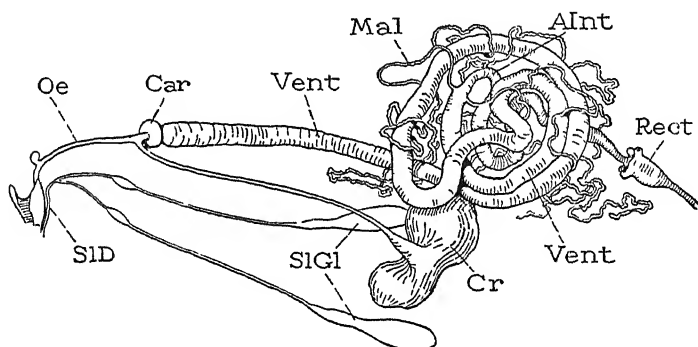
FIG 213 —The alimentary canal and its appendages of the apple maggot fly (*Rhagoletis pomonella*) showing the diverticular crop characteristic of the Diptera The liquid food in the crop usually contains quantities of living microorganisms In feeding, the fly frequently regurgitates the contents of the crop, a habit that is conducive to the spread of pathogenic microorganisms   *Oe*, esophagus, *Car*, cardiac valve, *SlD*, salivary duct, *SlGl*, salivary glands, *Cr*, crop, *Mal*, Malpighian tubules, *Vent*, ventriculus, *AInt*, anterior intestine, *Rect*, rectum   (*After Snodgrass*)

food materials and are then reingested   In this way, the surfaces fed upon are contaminated with whatever microorganisms are present in the crop   The soft-rot bacteria and the spores of the ergot fungi are disseminated in this way by several species of fly

The *proventriculus* is the terminal region of the stomodaeum, and its structure and function vary in different insects   In its simplest form, it is a narrow tube more or less invaginated into the anterior segment of the mesenteron, forming the cardiac valve that serves to regulate the passage of food from the crop into the ventriculus   The structure is somewhat more complicated in chewing insects that feed on solid material   The walls are often heavily sclerotized and armed with toothlike spines

that serve to hold the food particles in the crop without completely closing the entrance into the ventriculus   In this way, the digestive fluids of the ventriculus may flow forward into the crop and partly digest the food before it enters the mesenteron   In some insects, there is evidence that the proventriculus also serves as an organ for further trituration of the food, a so-called "gizzard" or "chewing stomach "

2 The Mesenteron —The mesenteron, or mid-intestine, is the middle segment of the alimentary canal and is the principal digestive organ of the insect   It is often called the *ventriculus* It is generally in the form of a long tube of uniform diameter and is usually not differentiated into distinct regions   In some insects, as in the muscoid Diptera, the anterior portion is differentiated into a flat circular region containing the cardiac valve and separated from the rest of the mesenteron by a constriction

The primary functions of the mesenteron are digestion and absorption   The epithelial layer of the walls of the mesenteron is much thicker than that of the stomodaeum   It is composed of large columnar cells of irregular length with ends projecting into the lumen   These are the digestive cells that secrete the digestive fluids and probably also absorb the digested foods   In some insects, there are two kinds of epithelial cell specialized for these two functions   The digestive cells are relatively unstable and are constantly disintegrating and being regenerated   The epithelium of the mesenteron is of endodermal origin and is not cast out when the insect molts

The food contents of the mesenteron of many insects are enclosed and separated from the epithelium by a thin transparent membrane known as the *peritrophic membrane*, the function of which is somewhat obscure   It is usually interpreted as a chitinous intima of the mesenteron secreted by the epithelial cells   In the Diptera, it is the product of a ring of specialized cells encircling the cardiac valve   The membrane is permeable to the digestive fluids and to the digested food materials

Blind pouches, or *caeca*, varying in number and shape are formed frequently as evaginations of the walls of the mesenteron They most commonly originate at the anterior end near the cardiac valve but often arise from other parts, and in some species there may be several sets of caeca arising from different sections of the ventriculus (Fig 214)   The functions of these gastric

caeca differ in different insects   In certain insects, they are
apparently secretory organs, but in others they act as receptacles
for congenitally transmitted symbiotic microorganisms, Glasgow
(1914), Buchner (1930), and others have studied the caeca and
their enclosed symbiotic microorganisms   In the Heteroptera,
the caeca with their symbiotic bacteria are especially common
These structures have assumed a position of importance in the
study of insects in relation to plant diseases   Relatively little
is known of the identity and function of the symbiotic micro-
organisms, but in several instances the caeca are known to harbor
plant pathogenic species   The gastric caeca and their symbiotic
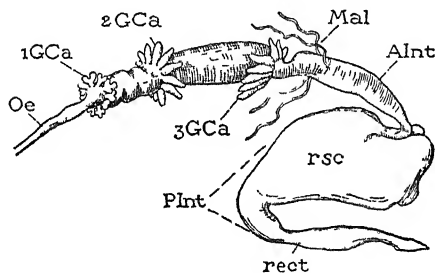
Fig 214 —The alimentary canal of a scarabaeid larva (*Popilla japonica*)
with three sets of gastric caeca (1*GCa*, 2*GCa*, and 3*GCa*)   The gastric caeca
usually serve as reservoirs of symbiotic microorganism which in some insects are
plant pathogens   *Oe*, esophagus, *Mal*, Malpighian tubules, *AInt*, anterior intes-
tine, *PInt*, posterior intestine, *rsc*, rectal sac, *rect*, rectum   (*After Snodgrass*)

microorganisms should be studied more thoroughly from this
viewpoint   For a more complete discussion of the question, see
Chap III
    The epithelial cells of the larval mesenteron are cast off and
renewed by a layer of regenerative cells during metamorphosis
It is of interest to recall that, despite this renewal, bacteria may
survive in the mesenteron of certain dipterous insects during
pupation and ensure the contamination of the newly emerged
imago (Leach 1933)
    A striking modification of the alimentary canal occurs in the
Homoptera, producing a structure known as the *filter chamber*
(Fig 215), formed by two distant parts of the digestive canal
which are closely applied to each other and bound in place by a
sheath of connective tissue   The parts bound together to form
the filter chamber are usually the two ends of the mesenteron,
often including also the anterior end of the proctodaeum   The

Homoptera are chiefly insects that feed on plant sap and, in order to get an adequate supply of the necessary nitrogenous food materials, usually ingest a great excess of water and soluble carbohydrates   The filter chamber is a device to permit the rapid elimination of the excess water and sugars which diffuse directly from the anterior region of the ventriculus into the proctodaeum, the nitrogenous and fatty foods being retained in the ventriculus for digestion and absorption   The sugar solutions eliminated in this way form the so-called "honeydew" commonly produced by many homopterous insects
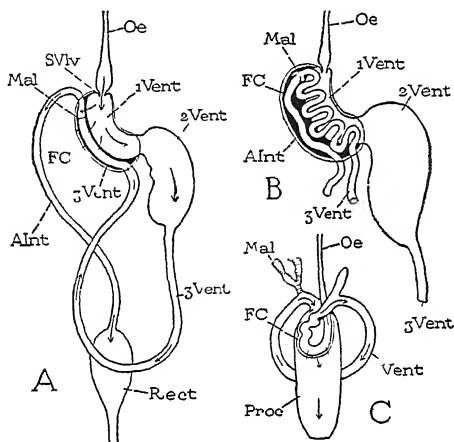
FIG 215 —The filter chamber of Homoptera   *A, B,* and *C,* three types of differing degrees of complexity   (*After Snodgrass*)

The honeydew, being rich in sugars, is a good medium for the growth of microorganisms and is concerned in the development of a number of injurious plant diseases   The so-called "sootymold" diseases are caused by fungi growing in honeydew that falls upon the leaves   The fungus growth is often so heavy that it interferes with the normal functions of the leaves, greatly injuring the plant   There is no evidence to show that the honeydew from viruliferous insects is of importance in the transfer of virus diseases   The virus particles apparently are unable to diffuse through the membrane of the filter

3 The Proctodaeum.—The proctodaeum, or hind-intestine, like the stomodaeum, is of ectodermal origin, and its epithelium is cast out and renewed each time the insect molts   In its simplest form, the proctodaeum is a plain tube connecting the

mesenteron to the anus, but in most insects it is differentiated into several distinct regions   The point of union between the mesenteron and the proctodaeum is usually somewhat constricted, forming a *pyloric valve* that regulates the flow of materials from the mesenteron   The pyloric valve is generally of proctodaeal origin although, in some insects, it may be supplemented by a valve composed of mesenteric tissue, known as the *ventricular valve*

Two main divisions of the proctodaeum usually are recognized the *anterior intestine,* and the *posterior intestine,* or *rectum*   The former may be differentiated further into two regions on the basis of structure, these being separated by a constriction of the intestinal wall   The anterior segment is known as the *ileum* and the posterior as the *colon*   The primary function of the proctodaeum is to convey the residual products of digestion and the other waste products to the exterior, it is believed by some workers, however, that some absorption of foods takes place through the ileum   Absorption through certain modified regions of the proctodaeum of the termites appears to be the rule

The Malpighian tubules empty into the anterior intestine near the pyloric valve   These are long, slender, blind tubes formed as diverticula of the proctodaeum and serve as excretory organs They are immersed in the blood from which they remove the waste products of metabolism, especially urates and related compounds   In the larvae of some insects, the Malpighian tubules are modified to secrete a substance that is spun into silk threads with which the cocoon is woven   In other species, these organs function as caeca and harbor symbiotic microorganisms, The number of Malpighian tubules varies from 2 to more than 100 in different species of insects

The *posterior intestine,* or *rectum,* is that portion of the intestinal canal immediately preceding the anus   It is composed of a dilated rectal sac and a narrow segment leading directly to the anus   The rectal sac is sometimes asymmetrically expanded into a *rectal caecum*   On the interior walls of the rectum are found six or sometimes three rectal pads, or "glands"   They are outgrowths of the rectal epithelium composed of long columnar cells giving rise to protuberances into the lumen   The function of the rectal pads is not definitely known   Both secretory and absorptive functions have been attributed to them by different workers

ORGANS OF REPRODUCTION

The reproductive organs of insects often are concerned directly in the transmission of plant diseases They may be involved when the disease-producing agent is transmitted congenitally from one generation to the next in the vector or when the plant is inoculated by the vector in the act of oviposition Insects, with very few exceptions, are bisexual, the male and female germ cells occurring in separate individuals, but, in certain species, males are rare or absent, and parthenogenesis is not uncommon Since the male reproductive organs are rarely involved in the transmission of plant diseases, they are not included in the following discussion

The majority of insect species are *oviparous, i e*, the eggs hatch after oviposition There are, however, many species in which the eggs hatch within the body of the female just before oviposition and the young are extruded as larvae or nymphs This is called *ovoviviparous* reproduction True *viviparous* reproduction occurs only in a few species, if at all The method of embryonic development in the so-called viviparous reproduction of insects is fundamentally different from the viviparous reproduction of higher animals Yet, in some species of insects, the young undergo extensive development within the body of the mother insect For example, the larvae of the tsetse fly complete their development within the body of the female and pupate immediately after birth, being nourished before birth by the secretions of special glands

Both oviparous and ovoviviparous reproduction occur in the Aphididae In this family, ovoviviparous reproduction is usually parthenogenetic, the embryos developing in the egg tubes of the ovaries and being extruded as active nymphs In oviparous reproduction, the spermatozoa are stored in a receptacle of the female (the *spermatheca*) at the time of copulation, and the eggs are fertilized individually as they are extruded from the oviduct The embryo, therefore, develops outside the body of the female

For convenience, the reproductive organs may be considered as composed of two parts, the *internal genitalia* and the *external genitalia* The former harbor the germ cells, provide for their nutrition and development until they are ready for fertilization, and secrete the *chorion*, or shell They also include devices for storing the sperm and ensuring fertilization as well as glands for

secreting a protective matrix that covers the eggs, and they discharge the eggs from the body at the proper time   The external genitalia provide means for the copulation of the sexes and include special structures that enable the female to deposit the eggs in a suitable place for their subsequent development and survival

The *internal genitalia* of the female are made up of the following essential parts   (1) a pair of *ovaries,* (2) two *lateral oviducts* arising from the ovaries and converging into (3) a *median oviduct,* (4) a genital chamber, or *vagina,* (5) seminal receptacle, or *spermatheca,* in which the sperms are stored, and (6) a pair of *accessory glands* (Fig 216)

The *ovaries* usually consist of two groups of tapering tubes, the *ovarioles,* the number of which varies greatly in different species, four, six or eight in each ovary being the most common although they may be more numerous in certain groups   The germ cells are generated in the apex of the ovariole in the region known as the *germarium* situated just below the *terminal filament*   The germ cells pass into the larger part of the ovariole called the *vitellarium* where

Fig 216 —The structure of the female reproductive organs of an insect   *Lg,* ovarial ligament, *Ov,* ovary, *Ovl,* ovariole, *Clx,* calyx, *Odl,* lateral oviduct, *Odc,* median oviduct, *Gpr,* gonopore, *Spt,* spermatheca, *SptGl,* spermathecal gland, *AcGl,* accessory gland, *GC,* genital chamber (vagina) (*After Snodgrass*)

they are nourished by specialized nutritive cells and are transformed successively into *oogonia* and *oocytes* and into the fully developed but unfertilized egg   The epithelial layer of the wall of the vitellarium is composed of *follicle cells* that enclose each oocyte in a definite sac, or *follicle*   These cells secrete the *chorion,* or egg shell, and when no nutritive cells are present, they also nourish the developing oocyte

Three general types of ovariole are recognized on the basis of the method of oocyte nourishment   When there are no special

nutritive (nurse) cells, the ovariole is *panoistic*, when the nutritive cells are present, the ovariole is *meroistic* In the panoistic type, the nourishment is elaborated by the follicle cells and is absorbed directly by the oocyte In the meroistic type, there are special nutritive cells that nourish the oocytes by an active passage of the plasmic contents of the nurse cells into the cytoplasm of the oocyte In the meroistic type, the nutritive cells may be arranged alternately with the oocytes (*polytrophic*) or they may remain in the upper part of the egg tube, retaining
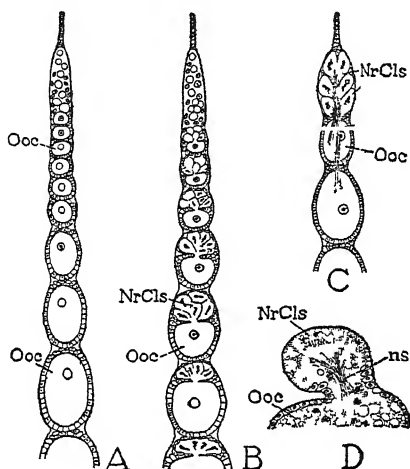
FIG 217 —Three different types of ovariole based on the method of oocyte nourishment *A*, panoistic type, *B*, polytrophic type, *C*, acrotrophic type, *D*, upper end of acrotrophic ovariole of *Pseudococcus* The method of egg formation and nourishment is of importance in the study of congenital transmission of plant pathogens by insect vectors *Ooc*, oocyte, *NrCls*, nurse cells, *ns*, plasmic strand (*After Shinji, from Snodgrass*)

connection with the oocytes by long protoplasmic strands (*acrotrophic*) (Fig 217)

The nature of the nourishment of the oocytes is of particular interest because in cases of congenital transmission of symbiotic microorganisms the actual transmission occurs at this stage "Infection" or contamination of the developing egg often takes place through the nurse cells or by direct invasion of the oocyte The process has been described by Brain (1923), Granovsky (1929), and others The problem of congenital transmission of viruses by the insect vector has assumed renewed importance by the proof of such transmission of the virus of the dwarf

disease of rice in the insect vector *Nephotettix apicalis* Since some viruses are transmitted through the egg and others are not, this stage of insect reproduction will be of critical significance in a study of insect transmission of viruses

The two *lateral oviducts* are ducts into which all the ovarioles converge and into which they empty their eggs   In some species, the lateral oviducts are distended into large pouches (egg calyx) for temporary storage of eggs

The two lateral oviducts unite to form the *median oviduct* which opens into the vagina through a constricted opening, the *gonopore*   The gonopore regulates the discharge of the eggs from the oviduct into the vagina

The *vagina* is a cavity formed by an invagination of the body wall and has a chitinous lining   It functions as a copulatory pouch during mating and is sometimes known as the *bursa copulatrix*   It is continuous with the median oviduct, and the spermatheca opens into it dorsally near the anterior end   The external opening of the vagina is the *vulva* and serves both for copulation and for the discharge of the eggs

In some insects, the *bursa copulatrix* provides a place for the development of symbiotic microorganisms that are congenitally transmitted by infecting the eggs as they pass out in oviposition (Buchner, 1930)   In other species, the vagina and the rectum converge so that the posterior regions of the vulva and the anus are essentially identical   This modification has been shown, by Buchner (1930) and others, to be an adaptation to ensure the contamination of the eggs with symbiotic microorganisms from the intestinal tract   In insects with this modification, the microorganisms usually are harbored in a number of irregular pouches in the dorsal wall of the rectum   The egg in passing through the oviduct presses against the pouches and forces the microorganisms out onto the surface of the egg   This condition is well illustrated by *Dacus oleae* and its symbiotic bacteria described in Chap VI (Figs 88, 89, and 90)

The *spermatheca* is a receptacle for storage of the sperms received during copulation   The sperms are ejected from the spermatheca upon the eggs as they pass from the oviduct   It is primarily an invagination of the ectodermis and is lined with chitin   It is essentially a single organ but may be variously branched   It is usually sacklike and is connected with the vagina by a slender

tube   A *spermathecal gland* is usually associated with the
spermatheca   It is formed as a diverticulum of the spermathecal
duct and secretes a fluid in which the sperms are discharged   In
some species of insect, symbiotic microorganisms are found in
the spermatheca along with the sperms, and congenital trans-
mission is affected by contamination of the egg at the time of
fertilization (Buchner 1930, Mansour 1934*a*)

The *accessory glands* are paired structures opening into the
vaginal chamber through its dorsal wall   The glands usually
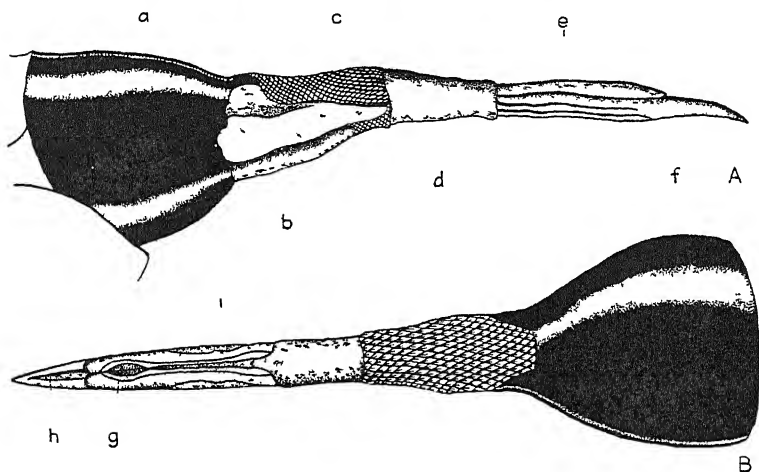
Fig. 218 —The ovipositor of *Rhagoletis pomonella*, the apple maggot fly
The sharp point of the ovipositor makes a puncture through the skin of the
apple through which the eggs are inserted   Along with the eggs are inserted
pathogenic bacteria that cause a decay of the ripe fruit and that also aid in the
nourishment of the larvae   See Figs 92 and 93   *A*, lateral view of extended
ovipositor, *B*, ventral view, *a*, seventh abdominal segment, *b*, pleural membrane,
c, basal sheath, *d*, distal sheath, *e*, ventral process, *f*, dorsal process, *g*, opening
of cloaca, *h*, ventral groove, *i*, lateral groove   (*After Dean*)

secrete an adhesive substance for attaching the eggs to the sub-
strate or for gluing several eggs together in a single mass   They
are often called *colleterial glands*   In the stinging Hymenoptera,
one of the accessory glands secretes the toxic substance associated
with the stinging apparatus

The *external genitalia* of the female insect consist of structural
adaptations for the deposition of eggs   Collectively, they con-
stitute the *ovipositor* and are derived from appendages of the
eighth and ninth abdominal segments (Fig 218)   The ovipositor
enables the insect to deposit her eggs in the most suitable place

for hatching and for the subsequent development of the larvae
This organ is of particular interest to the student of insect trans-
mission because it is used by many insects for inserting eggs into
the tissues of plants (Fig 90)   The wounds made in oviposition
are frequently the avenues of infection of plant pathogens   The
oviposition wounds are especially important when the insect is
also an agent of dissemination of the inoculum   The oviposition
wounds made by the snowy tree cricket and by the apple-maggot
fly function in this way (see Chaps VI and VII)   In many
insects, the ovipositor is absent or greatly reduced, and the eggs
are extruded and attached to smooth surfaces or introduced into
naturally occurring cracks or crevices

The size and shape of individual parts of the ovipositor vary
greatly with different species according to the place of oviposition
and the work to be done by the ovipositor   In most of the species
that insert their eggs in the tissues of plants, the parts are provided
with sharp sclerotized points that are well adapted for making
the necessary punctures   There are some insects, however (as
the Cerambycidae), which make the necessary puncture with
their mouth parts after which the eggs are inserted with the
ovipositor

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THE INOCULA OF PLANT PATHOGENS IN RELATION TO INSECT DISSEMINATION

Plant pathogens produce many kinds of inoculum which are disseminated in many different ways. A consideration of the various kinds of inoculum and their adaptability to insect dissemination is helpful in a study of the relation of insects to plant diseases. Some kinds of inoculum are well adapted to wind dissemination, and others seem to be poorly suited for dispersal by wind but especially adapted to insect dissemination, still others may be adapted to dissemination by water or other agencies. With increasing knowledge of the methods of spore dispersal in fungi, it is even more evident that the various specialized methods of spore formation and liberation are very closely correlated with some equally effective means of dissemination. The nature and method of production of inoculum by a pathogen usually indicates clearly its most frequent method of dissemination and often leads to a better understanding of the disease.

Inoculum may be defined as that part, or developmental stage, of a pathogen capable of initiating a disease when placed upon the infection court under the proper environmental conditions. Spores of fungi and vegetative cells of bacteria are the most frequently observed units of inoculum although other structures may sometimes function. Inoculum may have important functions other than the initiation of a disease. Dissemination of the pathogen from place to place is one function, and consequently inoculum is usually composed of very small units that are easily disseminated by various agencies. Survival during periods of unfavorable environment and subsequent reproduction is another important function of inoculum. Therefore, much inoculum consists of units that are resistant to various unfavorable conditions such as desiccation, bright sunlight, and high or low temperatures. A third important function is that of multi-

plication   Very rapid multiplication is accomplished by the
production of extremely large quantities of inoculum by a single
individual

Plant pathogenic fungi may reproduce either sexually or
asexually   Some of those which reproduce sexually are homo-
thallic, both male and female gametes being produced on the
same mycelium   Others are heterothallic, each individual form-
ing only one kind of gamete   Heterothallic plant-pathogenic
fungi usually produce spores which on germination give rise to
haploid mycelium that must fuse with another mycelium of
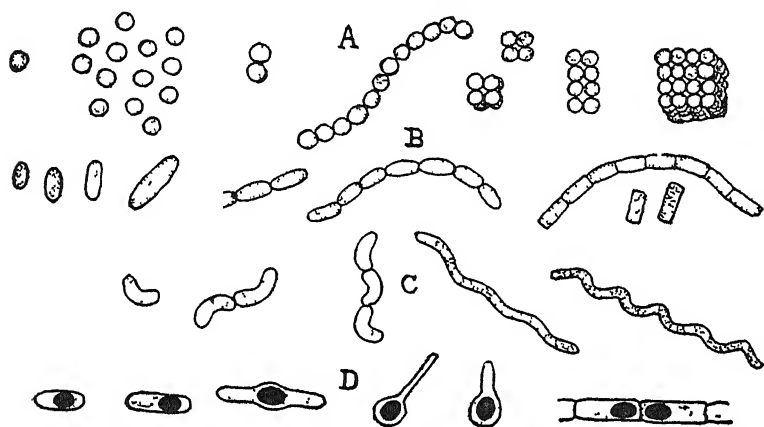
Fɪɢ 219 —A diagram of the three morphological groups of the true bacteria
A, Coccus type, *B*, Bacillus type, *C*, Spirillum type, *D*, bacterial spores   Prac-
tically all the plant pathogenic bacteria belong to the Bacillus type   Spores are
of very little significance as inoculum in bacterial diseases of plants   The
vegetative cells constitute the principal inoculum   (*After Heald*)

complementary sex before completion of the entire life cycle
Thus spores may, in some cases, serve as gametes as well as
inoculum

The most important plant pathogens fall within the following
four groups (1) bacteria, (2) fungi, (3) protozoa, and (4) filterable
viruses   The inocula of the different groups will be discussed
separately

Bacteria —The morphology of the plant pathogenic bacteria
is relatively simple, and only a few different kinds of inoculum
are produced (Fig 219)   The vegetative cells of bacteria con-
stitute the most common inoculum, only a few less important
bacterial plant pathogens produce spores although many species

of bacteria that are not pathogenic to plants produce them abundantly   Some of the plant pathogenic bacteria are said to have a filterable stage in which the organisms survive in units of submicroscopic size, but the significance of this stage of the bacteria, as inoculum, is not well known

From the standpoint of size, the bacterial cell is well adapted to insect dissemination   An average cell of the bacterial plant pathogens would measure less than 1 micron in width and not more than 2 microns in length, being small enough to pass readily through the mouth parts of practically all plant feeding insects, even those with special structures for screening out solid materials   The size of the food channel of the small sap-sucking Homopterous insects is not a limiting factor, for it is rarely, if ever, less than 1 micron in diameter and is usually much larger

The vegetative cells of plant pathogenic bacteria are variable in their resistance to unfavorable environmental factors, but they are more hardy than their simple structure and the lack of resistant spores would lead one to expect   Almost all plant pathogenic bacteria develop in an exudate or ooze composed partly of the plant sap and partly of products of bacterial metabolism (Fig 67)   It has been shown in numerous cases that the exudate has a decided protective effect on the bacterial cells   This is especially true in respect to desiccation   When they are subjected to dry conditions, the exudate surrounding the individual cells acts as a hydrophilic colloid having a high water-holding capacity that prevents injury by excessive desiccation

Bacterial exudate is usually of a sticky consistency so that it adheres readily to the body of insects coming in contact with it   In this way, bacteria are disseminated on the exoskeleton of the insects and are not in danger of being destroyed by desiccation   Moreover, bacterial exudates often give off odors attractive to insects, and many exudates have much food value and are eagerly ingested by insects   These properties are all conducive to the frequent dissemination of bacterial plant pathogens by insects   .

The fate of bacteria ingested by insects has not been extensively studied   However, the available evidence shows clearly that it is not always the same for all   Some bacteria are killed and digested in the alimentary canal of insects, others are more

resistant and survive, to be passed out in a viable condition in the excreta, still others are adapted to life in the insect body where they grow and multiply. It has been demonstrated that several species of bacteria that are pathogenic to plants are able to survive passage through the intestinal tract of their insect vectors. *Erwinia carotovora* and the seed-corn maggot, *E. amylovora* and fruit flies, *E. tracheiphila* and the cucumber beetle, and *Phytomonas savastanoi* and the olive fly are a few of the better known examples of bacterial plant pathogens that survive passage through the alimentary canals of their respective vectors. Although it is known that some bacteria thrive in the intestinal tracts of insects and others do not survive, very little is known about the factors that influence survival. This should be a promising field of investigation. The ability to survive and grow in the body of insects obviously is an adaptation favorable to insect dissemination and is a point that should not be overlooked in the study of vectors of bacterial diseases.

Insects, in addition to disseminating the bacteria, may provide them with a considerable degree of protection against environmental conditions. As pointed out in Chap. III, many bacteria, including some plant pathogens, live in a state of mutualistic symbiosis with insects, a condition that is especially conducive to insect dissemination. Bacteria that are adapted to survival in the insect's body during metamorphosis or hibernation have a distinct advantage over similar forms that are subjected to the more variable and hazardous environment elsewhere.

Spores are so rarely formed by plant pathogenic bacteria that it is scarcely necessary to consider them here. Their small size and extreme resistance to the environment would make them well suited to either wind or insect dissemination.

Pleomorphism is now recognized as a normal character of many bacteria. Filterable stages in which the bacteria exist in extremely small ultramicroscopic particles are not uncommon among plant-pathogenic species. It is not known that these filterable forms have any direct bearing on the problem of insect transmission, but, in examining insects for the presence of plant-pathogenic bacteria, failure to find visual evidence of the usual rod forms should not be considered as final proof of the absence of bacteria. Tests should be made for the presence of the pathogen in filterable form.

When all these factors are considered, it is evident that bacterial plant pathogens have many attributes that favor dissemination by insects   Several of the most destructive bacterial plant diseases are dependent almost entirely upon insects for transmission, and insects are known to spread others to a lesser extent   The methods of dissemination are still obscure for many others   Any insect that is a fairly constant visitor to plants affected with bacterial diseases should be looked upon with suspicion

Fungi —Three general types of inoculum are formed by fungi vegetative mycelium, sclerotia, and spores   Vegetative mycelium as inoculum is not particularly well adapted to insect dissemination   It may serve as inoculum when it survives in seeds or plant parts used in vegetative propagation   The mycelium in plant parts that are eaten by insects is potential inoculum   Taubenhaus and Christensen (1936) have shown that *Fusarium vasinfectum,* the cotton-wilt pathogen, may be disseminated in the fecal pellets of grasshoppers and other insects that ingest infected tissues   The same authors (1936), on the other hand, have shown that neither the spores nor the mycelia of *Phymatotrichum omnivorum* survive passage through the intestinal tract of three species of soil-inhabiting insects   Larvae of *Phyllophaga sp* and adults of *Blapstinus fuscus* and *Harpolus sp* were fed on vegetative mycelium and on spores of the fungus, but viable cultures could not be recovered from the intestinal contents or from the fecal pellets   Insects that feed in decaying wood are potential vectors of vegetative mycelium that may serve as inoculum although there has been very little study of the possibility

Many fungi form dense compact aggregates of hyphae filled with oil globules and other reserve foods   These structures are called "sclerotia," and they function chiefly as storage organs to aid in surviving unfavorable periods but also serve as inoculum, frequently being disseminated with seed or other plant parts   Because of the large size of most sclerotia, they are poorly adapted to insect dissemination and must depend on other agencies

Spores are the most common type of fungus inoculum   There is a marked diversity in the kinds of spore formed, and many kinds are extremely well adapted to insect dissemination   A

fungus spore consists of one to several specialized cells and serves
as a unit of reproduction and dissemination   Spores are usually
resistant to the environment and aid in the survival of unfavor-
able conditions   They vary in size from approximately 1 to
200 or 300 microns in diameter, although the majority would
probably measure less than 25   In size, as well as in many other
respects, fungus spores are similar to pollen grains and are
equally well adapted to insect dissemination
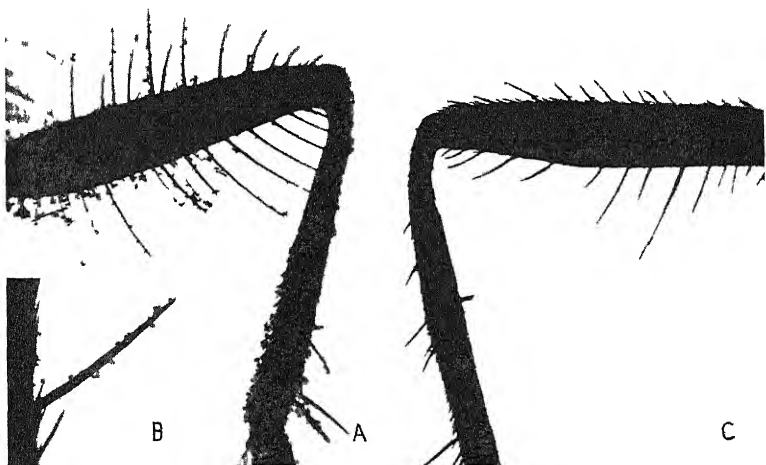
FIG 220 —The adherence of dry spores to the body of an insect   *A*, a leg of
a fly that was brought in contact with a quantity of dry fungus spores on a glass
slide, showing the spores adhering to the bristles, *B*, a single bristle more highly
magnified, showing the loose attachment of individual spores, *C*, a leg from the
same fly before contact with the spores

Spores adhere readily to the legs, wings, bristles, and other
parts of the insect body   Some spores are borne in a sticky
liquid matrix that may facilitate adherence to the bodies of
insects (Figs 43, 99, and 221), but dry spores will adhere almost
as well   This fact may be readily demonstrated by bringing
the leg or wing of an insect in contact with dry spores of any
common fungus and observing it under the microscope (Fig 220)
Not only do the spores adhere readily to the insect organ, but
also they may be brushed off easily   The force responsible for
the adherence of spores in this way is not clear although it may
be in part the attraction of the thin films of water that are

known to exist on the surface of apparently dry bodies   It has
been shown that it is not entirely a matter of electric charges
This phenomenon of adherence of dry spores to dry surfaces is
discussed at some length by Hanna (1924) in connection with
the dry-needle technique of picking up single spores   Hanna
demonstrated that dry spores would adhere readily to dry needles
regardless of the electrical charge of the needle   The force of
adherence is not great, and the spores are easily dislodged   What-
ever the explanation may be, the ready adherence of dry spores
to dry surfaces adds to the ease with which they are disseminated
by insects

Fungus spores are notably resistant to environmental condi-
tions   The resistance may be caused by the nature of the
protoplasm, by a thick wall, by a hydrophilic sheath, or by a
hydrophilic matrix in which they are borne   Many fungus spores
are resistant also to the environment found in the intestinal canal
of insects   In the majority of cases where the question has been
investigated, spores have been found to pass through the intes-
tinal tract of insects uninjured   One significant exception was
pointed out by Taubenhaus and Christensen (1936) who fed
Fusarium vasinfectum to a large number of insects   The fungus
passed uninjured through all the phytophagous insects but did not
survive passage through any of several mycophagous insects
This would suggest that the digestive juices of insects which
normally feed on the tissues of higher plants are less injurious
to fungus spores than those of insects which commonly feed on
fungi

A significant relationship between insects and fungus spores
was reported by Schneider-Orelli (1911), who found that spores
of the ambrosia fungus associated with *Xyleborus dispar* would
not germinate when taken directly from the tunnels in the
wood but germinate readily when recovered from the crop of
the beetle   It was suggested that something in the intestinal
contents of the beetle served as a stimulus to germination   A
period of dormancy during which spores will not germinate is
common for many fungi   The factors responsible for breaking
the dormancy are obscure   Should the fungus be closely associ-
ated with an insect, it would not be unreasonable to look for the
stimulus in the insect's body   Similar relationships between
fungi and higher animals have been described by Massee and

Salmon (1902) and Buller (1934) in their studies of the coprophilous fungi   Many of these fungi which are normally found only on dung produce spores that do not germinate until they are eaten by animals and are passed out in the dung where they germinate readily and abundantly
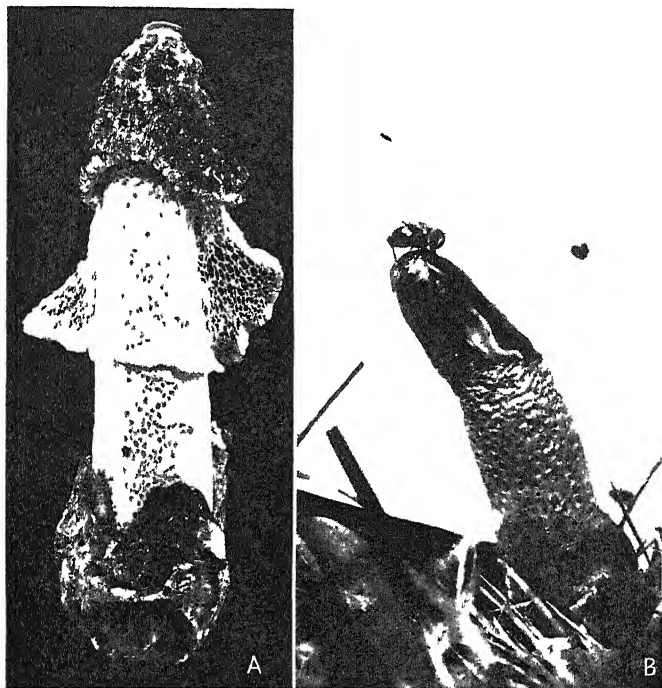
FIG 221 —Stinkhorn fungi   *A*, a typical sporophore of *Dictyophora duplicata* showing the shining black sticky mass of spores and the lacelike veil, *B*, a fly feeding on the sticky mass of spores of *Mutinus curtisii*   The stalk of this fungus is bright rosy red, the spore mass is brown

It is not necessary here to describe the many different kinds of spore formed by fungi as this information can be obtained from any standard mycological text   It will be sufficient to consider a few examples in which the methods of spore production and liberation show some special adaptation to insect dissemination

A number of pathogenic fungi form their spores in a matrix that is attractive to insects   *Claviceps purpurea*, the ergot fungus, produces its conidia in a drop of sugary solution that is

eaten greedily by many insects, especially flies which also visit healthy flowers in search of pollen, thus serving as effective vectors of the fungus   The sugary solution has a characteristic odor that seems to attract the insects   These characters must be considered as adaptations on the part of the fungus that ensure insect dissemination of its spores

A similar adaptation is shown by the stinkhorn fungi, which produce their spores in a sticky matrix with a foul, carrionlike odor (Fig 221)   Flies are attracted to the matrix, feed upon it, and effectively disseminate the spores that adhere to their bodies The spores may pass uninjured through the digestive tracts of flies, and they are probably disseminated also in this way   This adaptive relationship has been studied and discussed at considerable length by Fulton (1889) and Cobb (1906, 1909)   Fulton described the morphology and growth habits of a large number of these fungi and made extensive observations and experiments dealing with spore dissemination by insects   In concluding his discussion he states

In the Phalloidei then it can scarcely be doubted that we have a group of fungi which have undergone great modification so as to become adapted for the dispersion of their spores by the agency of insects and especially by those which habitually affect putrid substances, and would therefore deposit the spores on the most suitable nidus for their growth   It is an example of the substitution of the more certain action of insects for the uncertain action of the wind, just as in the case of the cross-fertilization of flowers, where the former agency has so largely replaced the latter

The chief adaptations shown by the Phalloidei in this respect were summarized as follows

(1) The formation and maturation of the spores within a closed volva, usually subterranean and protected largely from injury

(2) The sudden emergence and expansion of the receptacle, not by the comparatively slow process of cellular growth, but by a mechanical springlike apparatus acting quickly

(3) The freely exposed hymenium undergoing rapid mimetic changes, whereby putrid matters are simulated in color, consistency, and usually odor

(4) The development of a striking form, and of such colors as will make the receptacle most conspicuous, and the production of accessory parts for the same purpose

(5) The rapidity of the whole cycle of phenomena by which the risk of accidental destruction, by animals, etc , is lessened, and the effective dispersion of the spores secured

Fulton concluded his discussion with the following significant remarks concerning the teleology of putrefactive odors in general

I may finally add a word as to the importance of these observations that flies and other insects transport living spores of fungi in relation to the transport of bacteria   The teleology of the bad odors of putrefaction has, so far as I am aware, never been explained, but since these odors depend upon the presence of organisms, and serve to attract multitudes of flies, and since it is a rule in Nature that no organism aids another except, so to speak, with the object of ultimately benefiting itself, it seems to me highly probable that the odor of putrescent matter has been developed in relation to the visits of flies   The advantage to the bacteria is obvious, for by the odor produced, the irregular fortuitous action of the wind is largely replaced by the direct purposive action of insects, and hence, once the odor is developed, flies will form the chief means of dispersal   It has been shown above that spores may retain their vitality during their passage through the digestive canal of flies, and there can be little doubt the same applied to bacteria   Flies may thus serve to disperse not only the microorganisms associated with putrefaction, but also those which are the cause of certain diseases, such as anthrax, etc , in which the products are attractive to them, and since flies, apart from their own powers of locomotion, are known to be carried long journeys in railway trains and steamers, they may serve to carry infection and spread diseases to distant places

Cobb (1906, 1909) has elaborated on this phenomenon of spore dispersal by flies and has supplied additional evidence based on observations and experiments with *Ithyphallus coralloides*, a stinkhorn fungus that he erroneously thought to be the cause of a root rot of sugar cane in Hawaii   Cobb showed that the spores of this fungus were not injured by passage through the digestive tract of flies   He showed by actual spore counts that a single "flyspeck" often contained as many as 22,400,000 spores of the fungus

The blue-stain fungi (*Ceratostomella spp*) appear to form their spores in a manner that makes them better adapted to dissemination by the bark beetles than by any other means   Both the conidia (*Graphium*) and the ascospores are produced under the bark in sticky solutions that make them unsuited to wind dissem-

ination (Figs 102, 103, and 104) The most abundant sporulation occurs in the tunnels and pupal chambers of the bark beetles, the sporophores and perithecia pointing toward the center of the tunnels in such a way that the spore masses are in the most advantageous position for coming in contact with the insects (Leach, Orr, and Christensen, 1934)

Many Ascomycetes liberate their ascospores by forcibly ejecting them from the asci This process has been described fully by Buller (1909, 1934) and others As the asci mature, they

Fig 222 —Apothecia of *Sclerotinia sclerotiorum* in the act of discharging ascospores by the puffing process Note the white cloud of spores against the black background (*After Dickson and Fisher*)

imbibe water and develop considerable internal pressure The ascus wall near the apex becomes soft and stretches until it suddenly gives way, releasing the pressure which forces the ascospores and the surrounding liquid out into the air The liberation usually occurs as a series of sudden discharges, a phenomenon known as "puffing" The ascospores are forcibly ejected into the air for several centimeters, forming a white cloud of spores which may be carried off by air currents (Fig 222) This process is usually interpreted as an adaptation to wind dissemination although the spores may not be disseminated exclusively by wind The sudden discharge of spores may be set off in several different ways Falck (1916, 1923) has classified

the discomycetes into two groups on the basis of the stimulus required for puffing   One group discharges its spores when warmed by radiant heat as from the sun, the other group responds to a slight touch of the fruiting body such as would be supplied by an insect alighting upon it   An insect alighting upon a ripe fruiting body would, by providing the stimulus for the spore discharge, become thoroughly contaminated with spores   It appears as if the puffing mechanism may not exclude the possibility of effective insect dissemination

A striking example of adaptation of a fungus for insect dissemination is found in the anther smut of pinks [*Ustilago violaceae* (P) Fckl] as described by Brefeld and Falck (1905)   This smut affects several species of plant of the pink family   Infection is accomplished through the flowers by spores that germinate on the stigmatic surface   The fungus is systemic and invades the entire plant, but spores are formed only in the anthers where they replace the pollen grains   The dark-colored echinulate smut spores are approximately the same size as the pollen grains, and, although they may be wind-disseminated, they are as readily transported by insects   The flowers are commonly pollinated by insects, especially by certain species of sphinx moths   The moths, in visiting flowers on infected plants, become contaminated with smut spores along with the pollen grains and transport them to the stigmas of healthy plants where they germinate and infect   Thus, by its habit of sporulating in the anthers, the fungus has become adapted to the more certain method of dissemination by the same insects that pollinate the flowers of its host plant

A somewhat similar adaptation was described by Silow (1933) in a systemic disease of red clover caused by *Botrytis anthophila* Bond   The spores of this pathogen are disseminated by the bees that pollinate red clover   The spores, along with the pollen grains, are deposited on the stigma where they germinate and infect   The mycelium of the fungus grows into the developing seed and persists under the seed coat without affecting the viability of the seed   When the infected seeds germinate, they give rise to systemically infected plants   The fungus grows out into the young flowers, many of which are blighted, and the spores are formed over the surface of the shriveled anthers (Fig 125) Bees on visiting the blighted blossoms in search of nectar become

contaminated with spores and in the continued search for nectar spread the infection to other plants

Protozoa —A few protozoa are recognized as plant pathogens The methods of dissemination of endophytic protozoa have not been extensively investigated, but all available evidence points to insect transmission as the general rule   DuPorte (1924) mentioned two laticiferous plants (*Asclepias syrica* and *Convolvulus sepium*) in which the protozoa were seed-transmitted   No spores suitable for wind dissemination are produced by the protozoa   The endophytic protozoa appear to grow and multiply within the body of certain insects (Franca 1920*a*) and to this extent may be considered as well adapted to insect dissemination In fact, the nature of the organisms would make it difficult to account for their dissemination in any other way   When found in plant tissues, they occur only as intracellular parasites in the living latex cells   Since the latex cells are not exposed to the surface of the plants, it would be difficult to conceive of any other way in which the protozoa could gain entrance   In all probability, it will be found that practically all these endophytic protozoa are disseminated exclusively by insects   For a more complete discussion of insects and the endophytic protozoa see Chap X

Viruses —The exact nature of the inoculum of viruses is not known   Whatever the inoculum may be, it exists in extremely small particles suspended in the protoplasm of the cell   That it is well suited for insect dissemination is evident from the fact that so many viruses are insect-transmitted   Many are transmitted only by insects so far as we know   It has been shown that infection by viruses depends upon the virus particles coming in contact with the living protoplasm in the cells or with the plasmodesmid strands connecting the cells   The sucking insects are ideal agents for introducing the virus into the living cells with the minimum exposure of the virus to unfavorable conditions

Certain viruses are capable of surviving for long periods in the body of the insect vectors, and there is some evidence that a few of the viruses may actually increase there   These properties of the virus particles all add to the effectiveness with which they may be disseminated by insects   The extent to which the inoculum of viruses is capable of resisting desiccation, oxidation, and other unfavorable factors of the environment varies widely

and greatly influences their normal means of transmission   The virus of tobacco mosaic, for example, is very resistant to desiccation and may survive for many years in dried leaves, while the virus of cucumber mosaic will survive only a few hours of dryness   In general, those viruses which are unable to survive for very long *in vitro* are more dependent upon insects for transmission

Seed Plants.—There are a few well-recognized plant pathogens among the seed plants   The common field dodder (*Cuscuta spp*) and the mistletoes (*Loranthaceae*) are among the better known groups   The seeds formed by these pathogens are too large to be disseminated by insects, but the seeds of the mistletoes are especially adapted to dissemination by birds

The seeds of the mistletoes are borne in a viscous and very sticky liquid that causes them to adhere tenaciously to anything with which they come in contact   The seeds adhere to the branches of the tree and germinate during rainy weather, sending haustoria into the xylem elements and absorbing water and mineral salts

In the dwarf mistletoe (*Razoumofskya spp*), the seeds are forcibly ejected from the berry and are disseminated locally in this way   As the berry matures, it develops considerable internal pressure until a slight disturbance causes it to explode and eject the seed   The seeds may travel as far as 33 feet in a horizontal direction as a result of this force   For dissemination over longer distances, they are dependent upon birds which eat the berries and regurgitate the seed or pass them out in the excrement   The sticky seed also may adhere to the bird's beak later to be wiped off upon a branch of a tree   The seed may be distributed for relatively long distances by birds, and many of them so distributed are deposited in places favorable for infection

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CHAPTER XV

THE FEEDING AND BREEDING HABITS OF INSECTS IN RELATION TO THE TRANSMISSION OF PLANT DISEASES

Insects constitute the largest of all animal groups, it having been estimated that approximately 75 per cent of all the animals of the world are insects. Nearly 700,000 species have been described and named, and it has been stated that there are probably several million species still undescribed. One finds an extremely wide variation in the life habits of such a large group of organisms. Even among the relatively small number of insects known to be concerned in the spread and development of plant diseases, we find such a variety of types in respect to their mode of life that very few generalizations can be made concerning their ability to transmit plant diseases. If we are to acquire a satisfactory knowledge of the general principles involved in insect transmission of plant diseases, it is desirable that we make a brief survey of some of the life habits of insects as they concern effectiveness in plant disease transmission. Inasmuch as the acts associated with feeding and breeding of insects are the ones most frequently involved in disease transmission, particular attention will be given to these activities.

THE FEEDING HABITS OF INSECTS AS RELATED TO DISEASE TRANSMISSION

In order to be an effective vector of a plant disease, an insect must visit, with a reasonable degree of regularity, both diseased and healthy plants. The mere association of an insect with diseased plants or the presence of inoculum on or in the insect's body is not sufficient justification for concluding that the insect is a vector of the disease. Unless the insect bearing the inoculum visits a healthy plant under conditions conducive to inoculation and infection, it may be of no significance in the transmission of the disease. Failure to recognize this fundamental principle

has been the source of frequent error in the study of insects in relation to the spread of plant diseases This was the chief basis of the criticism made by Craighead (1916) of the work of Studhalter and Ruggles (1915) dealing with insects as vectors of chestnut blight These authors demonstrated that a large number of insects collected from blight cankers were contaminated with spores of the blight pathogen and concluded that "they are important agents in the local dissemination of this disease" Craighead objected to this conclusion on the logical basis that most of the insects included in the study rarely visited or fed upon healthy trees

One must be cautious, however, in concluding that an insect which apparently is associated only with diseased plants does not visit or attack healthy plants, for if the insect is a consistent vector of the disease and the plant always becomes infected following the insect attack, the situation easily may be misinterpreted For example, it has been shown in work on potato blackleg and other bacterial soft rots that certain Dipterous insects, generally referred to as scavengers, are, in reality, responsible for initiating the decayed condition that is supposed to have attracted them A careful study of the habits of the insect throughout its life cycle must be made before it can be disregarded as a possible vector

It is generally recognized that ergot of cereals is transmitted by insects that feed upon the sugary exudate in which the conidia of the fungus are borne A very large number of different kinds of insect have been observed feeding on the exudate, but they are not all equally effective in transmitting the disease No accurate rating of the relative importance of these insects has ever been made, but it is known that several species of flies that are among the most common visitors to infected heads not only consume the exudate but feed also on the pollen of healthy heads These pollen-eating species would naturally be more effective vectors than those species which are attracted to the heads of rye by the fungus exudate and which visit healthy heads only incidentally

Another instructive example of the way in which the feeding habits of insects may influence the effectiveness of insects as vectors is furnished by the bark beetles that transmit the Dutch elm disease These insects, principally *Scolytus scolytus* and

S multistriatus, breed by preference in weakened or dying trees, rarely are they able to establish themselves in healthy vigorous trees   If it were not for the fact that the beetles feed for a period after emergence on the twigs of healthy vigorous trees, during which time they inoculate them with the pathogen, the disease would in all probability remain a relatively unimportant disease of unthrifty trees   But because of this feeding habit vigorously growing trees are inoculated and the disease becomes extremely destructive on elms regardless of their vigor   The native American bark beetle (*Hylurgopinus rufipes*) breeds also in infected elms and occasionally transmits the disease, but it is much less effective than the other bark beetles because it does not have the habit of feeding on the succulent twigs   However, according to Kaston and Riggs (1938), this species sometimes feeds upon the inner bark of the trees before breeding tunnels are established   The significance of this type of feeding in transmission of the disease has not been determined accurately, but there is reason to believe that it is of considerable importance (Kaston 1939)

It is of interest to note that the pine bark beetles (*Ips spp* and *Dendroctonus spp*) transmit blue-stain fungi that are capable of killing vigorous trees when artificially inoculated into them, but because the insects infest only weakened trees, the disease is largely confined to trees previously injured by some other cause   These beetles, unlike the *Scolytus* elm beetles, do not feed on the twigs   Transmission is accomplished entirely through the breeding tunnels

The Mechanics of Feeding —The mechanical process of feeding is a factor of prime importance in determining the effectiveness of an insect vector of a plant disease   Many insects that are frequent visitors to plants feed upon plant products but do not wound the plant in any way   As a general rule, these insects are not so effective as those which make feeding wounds, and yet some of them are important vectors   These usually transport the inoculum to blossoms or to wounds made by other agencies or else transport inoculum that does not require wounds for infection   The blossom-visiting insects are the most effective vectors of this class   As examples may be mentioned bees, wasps, and flies as vectors of fire blight, flies as vectors of ergot, and the sphinx moths as vectors of anther smut of pinks   Insects that transport inoculum to wounds made by other

agencies are, for the most part, incidental vectors and of minor importance   In such cases, wind or other agent of dissemination is usually of greater significance than insects although there are some important exceptions

Those insects which make feeding wounds are, by far, the more effective vectors of plant diseases   Many different kinds of wounds are made by insects in the process of feeding, and the type of wound is a factor of much significance in determining infection   No two species of insect feed in exactly the same way, and very minor differences may have a great influence on the effectiveness of the insect as a vector

Some of the more common types of feeding wound are those made by the chewing insects   These may consist of a simple crushing of plant tissue by such insects as grasshoppers, caterpillars, and many beetles, or they may take the form of burrows extending deep into the tissues, such as those made by wood-boring beetles   It would be difficult to make any generalizations as to which of these two kinds of injury is more conducive to insect transmission, much depends upon the nature of the disease being transmitted   In general, the feeding wounds made by such chewing insects as grasshoppers and potato bugs, because of exposure to the air, dry quickly and are relatively unimportant as points of infection   On the other hand, similar wounds made by the cucumber beetles on the stems of cucurbits are effective avenues of entrance for the vascular bacterial parasite *Erwinia tracheiphila*

Insects that burrow deep into plant tissues provide wounds that often are ideally suited for infection, although there are many exceptions   When the adult insects burrow into the plant, as do the bark beetles, many fungus spores are introduced and the tunnels provide ideal moist chambers for growth of the fungus and for infection   Other insects burrow in as young larvae, freshly hatched from eggs, and having had less opportunity for becoming contaminated are less likely to introduce inoculum   This difference may be illustrated by comparing the bark beetles that burrow in pine logs as adults and introduce large quantities of spores of the blue-stain fungi with the wood-boring *Monochamus spp* and the buprestid beetles which bore into the same logs as freshly hatched larvae and introduce few, if any, spores of pathogenic fungi

Chewing insects play a relatively unimportant part in the transmission of virus diseases This can be attributed largely to the type of wounds they make The cells bordering the wounds made by chewing insects are usually crushed and killed so that a virus introduced into the wound would rarely come into contact with living protoplasm, a recognized requirement for infection by all viruses Insects of this type are capable of transmitting only those viruses which are very highly infectious, being readily transmitted by artificial sap inoculation

The rasping-sucking type of feeding, represented by that of the larvae of Dipterous insects, results in wounds well adapted to transmission of certain kinds of diseases This type of wound is usually made in succulent tissues favorable to infection by bacteria and fungi, and the larvae burrow into the tissues to avoid the injurious effects of light and desiccation The continuous nature of the wound tends to counteract the wound-healing properties of the plant tissues and affords an excellent opportunity for successful inoculation

The piercing-sucking insects make wounds that are ideally adapted to the transmission of plant diseases They penetrate deep into the tissues with their mouth parts, and any pathogen introduced into such a wound is not exposed to any of the ill effects of light, desiccation, or oxidation When the pathogen is transmitted biologically by the insect, the secretion of saliva into the wound provides a means of introducing the required quantity of inoculum It would, however, be unwise to generalize to any great extent as to the significance of the injection of saliva, for, as has been shown by Smith (1920), the capsid bugs are not capable of transmitting many of the plant viruses The saliva injected into the plant by these insects is highly toxic to plant cells and kills much of the tissue immediately surrounding the puncture Smith believes that the rapid killing of this adjacent tissue prevents the viruses from becoming established in the plant and is responsible for the failure of this particular group of sucking insects to transmit viruses effectively This conclusion is supported by the generally recognized fact that the viruses behave as obligate parasites and are not able to multiply except in direct contact with living tissue It is also possible that the saliva of some insects may be toxic to some kinds of inoculum

The mechanics of feeding by insects is of particular significance in the study of the transmission of the virus diseases   Brandes (1923), working with *Aphis maidis* and sugar-cane mosaic, was among the first to study the mechanics of feeding of insect vectors in relation to virus diseases, although as early as 1891
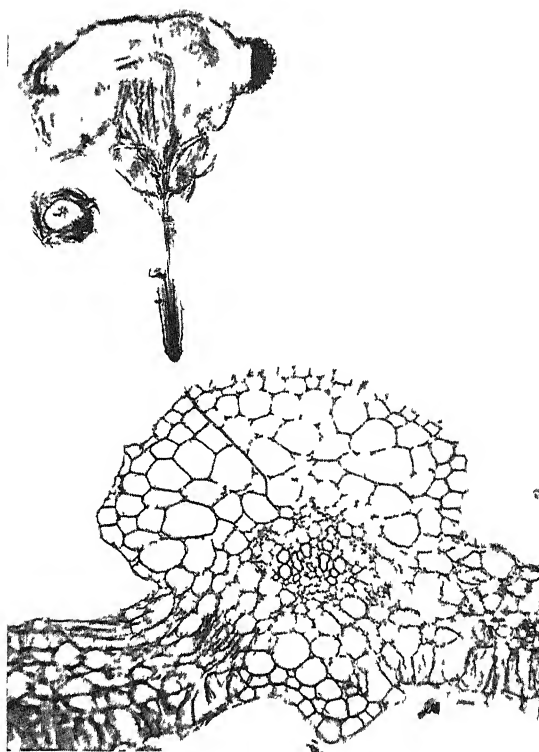
Fig 223 —A section through the head and mouth parts of an aphid feeding upon the vein of a potato leaf   Note that the setae have located and penetrated the phloem tissues   (*After Dykstra and Whitaker*)

Busgen had studied the methods of feeding of aphids in connection with his investigation of the formation of honeydew The feeding wounds of aphids (*Rhopalosiphum dianthi* Schrank) and the path followed by the setae were described also by Woods (1900) in his study of stigmonose of carnations   In 1923, Davidson described the penetration of plant tissues by *Aphis rumicis* L   In the same year, a similar study was reported

by Horsfall (1923) with respect to *A rumicis* L , *Myzus persicae*
Sulz , *Macrosiphum rudbeckiae* Fitch, and *M ambrosiae* Thomas
This was followed by the more extensive comparative study of
the feeding methods of several Hemiptera in particular relation
to virus transmission as reported by Kenneth Smith (1926)
The mechanism of feeding has been described for several leaf
hoppers by Smith and Poos (1931) and by Smith (1933), and
similar studies dealing with the beet leaf hopper [*Eutettix tenellus*
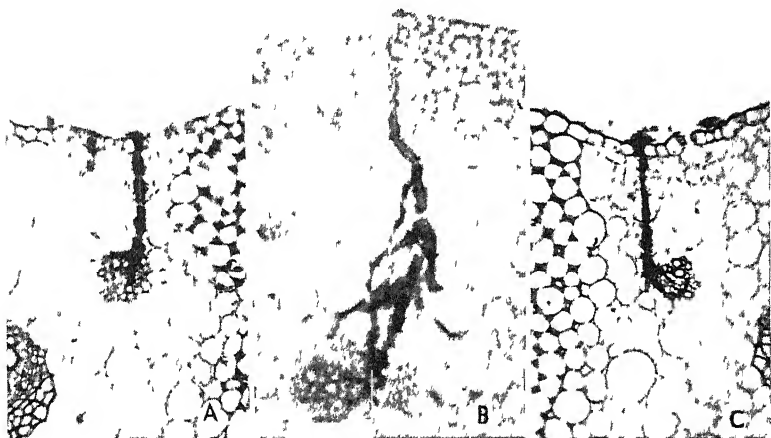
Fig 224 —Three sections through petioles of sugar-beet leaves at the point
of feeding punctures of *Eutettex tenellus*, showing the sheath of heavily staining
material that surrounds the path of the setae   Note the change of direction and
the results of probing to reach the phloem in *B*   (*After Bennet by courtesy of
the U S Department of Agriculture*)

(Baker)], with special reference to the transmission of curly top,
were made by Bennett (1934)

These studies, along with other less extensive ones, have given
us a fairly clear picture of the nature of the feeding punctures
of the most important groups of vectors of virus diseases   In
general, those Homopterous insects which are most effective in
transmitting viruses feed upon the phloem (Figs 223 and 224)
The stylets may penetrate the cell walls of the epidermis or may
push in between epidermal cells   Penetration of the cortex
parenchyma may be either intercellular or by direct penetration
of the cell walls   As a rule, the setae of aphids follow an inter-
cellular path although cell-wall penetration is often observed
The leaf hoppers, on the other hand, usually puncture a higher

percentage of the cortex cells in a more direct path to the phloem
The path followed appears to be determined largely by the size
and stiffness of the setae and the relative thickness of the cell
walls of the plant tissues fed upon

In the feeding of both leaf hoppers and aphids, there is a
copious flow of saliva into the intercellular spaces from the
beginning of penetration   This secretion reacts with the plant
sap and forms a sheath that completely surrounds the penetrat-
ing setae (Fig 224)   There has been a difference of opinion as
to the nature of the sheath material   Horsfall (1923) inter-
preted it as of plant origin, being formed as a wound reaction
However, the opinion of most workers is that the sheath is
largely of insect origin   Smith (1933) presented strong evidence
from microchemical tests to support this view, and Bennett
(1934) has observed the formation of a typical sheath of *E
tenellus* while feeding through a membrane on hanging drops of
a synthetic solution

The function of the setal sheath is not definitely known   It
has been suggested that it serves to make an airtight seal about
the setae, thus preventing the leakage of air or liquids along the
sides and increasing the efficiency of the pumping mechanism
used for sucking out the contents of the phloem   The sheath
also may serve to protect the setae from any injurious action of
the cell sap and may provide better lubrication for their move-
ment   There is also some evidence that the salivary secretions
aid the penetration of the smaller setae by dissolving the middle
lamellae of the cells   In any event, the feeding mechanism is a
very efficient one   Since it has been shown that the salivary
secretion of many vectors is the medium in which the virus is
introduced into the plant, a more perfect mechanism for inocula-
tion scarcely could be imagined

The mechanism of feeding is important, also, in the study of
the nonparasitic diseases caused by toxicogenic insects   Dis-
eases of this type (psyllid yellows, green spot of pineapple,
hopperburn, etc) have been attributed in general to diffusible
toxic substances introduced in the saliva of the insect   However,
this interpretation has been questioned in the case of hopperburn
by Smith and Poos (1931), Smith (1933), and Johnson (1934),
who maintain that the setal sheath, together with the mechanical
injury to the plant tissues, results in a clogging of the phloem

vessels that interferes with the normal translocation of plant materials and accounts for pathological symptoms of hopperburn   There is need for further study of the mechanics of feeding and associated phenomena in interpreting the nature of the diseases caused by toxicogenic insects

Food Plants —The choice of food plants by insects has an important bearing on their ability to transmit diseases successfully   Among the first things to be determined in a study of insect transmission is the host range of the disease and range of food plants of the insect in question   Practically all plant diseases affect to some extent one or more species of noncultivated plants which may serve as reservoirs for the pathogen   Weeds and other noncultivated plants rank among the most common sources of infection for the cultivated crop   Also, many insect pests of crop plants feed upon wild plants in some stage of their development or during some part of the year   Outbreaks of many insect-transmitted plant diseases can be traced directly to insects that move from infected wild plants to the cultivated crop   The movement may be simple dispersion from breeding centers or definite directional migration   This factor is especially important in respect to virus diseases, as may be illustrated by the curly top of sugar beet and *Eutettix tenellus*, the mosaic of cucurbits and *Aphis gossypii*, and many others   Even though the noncultivated plants may not be susceptible to the disease in question, they may serve as breeding places for the vectors, and a knowledge of this fact is equally important in the control of insect-transmitted diseases

Mader (1937) has reported that in New York the presence of yellow dwarf of potato transmitted by the clover leaf hopper (*Aceterogallia sanguinolenta*) is closely correlated with the presence of medium red clover (*Trifolium pratense*)   Since the leaf hopper is abundant in regions where the disease is not prevalent, the clover, which is a suscept of the disease, probably serves as a source of viruliferous vectors that move from the clover to potatoes   If this relationship is sufficiently constant, a change in cropping practices may be more effective in controlling the disease than attempts at direct control of the vector

Wellman (1935) has studied and charted the spread of southern celery mosaic by *A gossypii* Glov in relation to weeds as sources of infection   This virus affects many species of plants, including

weeds of various types, *Commelina nudiflora* L being the most important of its weed hosts   This is a perennial plant in which the virus overwinters and on which the aphids feed, especially when more tender annual plants are not abundant   Careful studies have shown that infection in celery starts from infected weed patches along the edge of the field and spreads progressively through the field

When the annual plants die or are chopped down, aphids leave and carry the virus back to nearby perennials, reestablishing themselves on old plants, or colonizing and infecting the young perennials, which act as reservoirs of the virus over periods unsuited to growth of the more tender plant species   It is upon advent of new growth of many of the annuals that dissemination of the disease becomes noticeable   The virus-carrying aphids migrate back from the less succulent and palatable reservoir hosts to annual crops and weeds, and the virus then becomes economically significant

A considerable degree of control of celery yellows has been demonstrated by the thorough local eradication of *C   nudiflora* in the vicinity of celery fields

Heinze and Profft (1938) made an extensive study of the life history and distribution of *Myzus persicae* Sulz in Germany in relation to the prevalence of virus diseases of potatoes   It was concluded that this aphis alone is responsible for the transmission of the three most important potato viruses in Germany (leaf roll, y and a virus) and that there is a close correlation between its abundance and the difficulty of producing virus-free seed stock   It was shown furthermore that the abundance of the aphis in various parts of Germany is largely determined by the abundance of peach trees   *Myzus persicae* is a polyphagous aphid, but it utilizes the peach exclusively as the winter host   In early fall, the winged form of the insect appears and migrates from potatoes (and its many other host plants) to the peach trees on which the sexual generation develops   Eggs are deposited on the peach trees in late October   They lie dormant until early spring, then hatch, giving rise to wingless females that reproduce viviparously   About 2 months later (approximately May 15 in Berlin), the winged individuals appear   Within a few days, these begin to migrate from the peach trees to potatoes and other summer host plants   Since the virus is not congenitally transmitted in the aphids from one generation to the next, the virus

must be acquired from infected potatoes or from systemically infected weeds

Extensive aphid counts in potato fields throughout the season in various sections of Germany showed clearly that *M persicae* was much more abundant in those regions where peach trees were more numerous and that these regions coincided with those previously recognized as unfavorable for the production of virus-free potatoes On the basis of these facts, it was recommended that seed-potato production be limited to those regions where peach trees are not economically important and that, in regions devoted to intensive seed production, as many peach trees as possible be eliminated

Murphy and Loughnane (1937), in a 10-year study of the spread of leaf roll in Ireland, state that *M persicae* winters in an active state on cabbage and that the relative freedom of potatoes from leaf roll in eastern Ireland is probably due to the absence of winter hosts of the aphids near the potato fields

Palmer (1938) has called attention to the importance of knowing the host range and relationships of aphids in respect to their role as vectors of virus diseases Aphids are grouped into the following three classes on the basis of their host relationships

Single-host aphids are aphids that feed upon only one species of plant or on a few closely related species of a single genus *A pomi* DeG on apple and *Macrosiphum rosae* (L) on rose are examples of this class

Polyphagous aphids infect a relatively large number of plant species in several distantly related families Examples are *A gossypii* Glov and *A medicaginis* Koch, each of which feeds on plants in 11 different families *Aphis rumicis* L and *M persicae* Sulz each feeds on plants in eight families These plants include both weeds and cultivated crop plants Vectors of virus diseases with polyphagous habits add greatly to the complexity of virus disease control

Alternate-host aphids commonly feed on a winter host, usually woody, and one or more herbaceous summer hosts For example, *M persicae* utilizes the peach as a winter host and feeds on many herbaceous species in summer *Aphis bakeri* Cowen winters on apple and feeds on clover in summer

The time of migration is often of great significance in the study of the relation of aphids to the spread and development

of virus diseases   *Alternate-host migrants* are those winged aphids
which leave the first host to migrate to the alternate one   The
migration usually occurs in late spring, but the exact date varies
with the species and with the climate   *Single-host* migrants
are the winged forms of the single-host aphids that are responsible
for the dispersion of the species on its preferred host plant   The
single-host migrants appear some time in late spring

It is well known that some aphids transmit only one plant
virus whereas other species transmit several different viruses
In general, it is the polyphagous aphids such as *M   persicae* that
transmit more than one virus   The single-host aphids as a rule
transmit only a single virus

The plants upon which toxicogenic insects have fed may
determine their ability to produce a disease as shown by Carter
(1936*b*) in his study of the green-spotting disease of pineapple
caused by the pineapple mealy bug [*Pseudococcus brevipes* (Ckl)]
When the insects were removed from *Panicum* grass to pineapple,
they failed to cause the greenspotting, but, when taken from any
other host, they readily caused the disease

The feeding habits of insects and their choice of host plants
are often influenced by cultural practices with striking effects
on their importance as vectors of plant disease   Thus, *A
maidis*, which is considered to be the principal vector of sugar-
cane mosaic, does not normally feed upon sugar cane but develops
abundantly on certain wild grasses that are preferred food plants
In the tropics, these wild grasses must be cut down periodically
as a cultural necessity   When this is done, the vector migrates
to sugar cane and in so doing transmits the virus from the wild
grasses   In subtropical regions, the wild grasses die in winter,
and then *A   maidis* feeds upon sugar cane until a new supply of
grasses is available   Ingram and Summers (1936) claim that in
Louisiana the rusty plum aphid [*Hysteroneura setariae* (Thomas)]
is the principal vector of sugar-cane mosaic although it does not
transmit the virus so readily as *A   maidis*   The sugar cane plant,
however, is a preferred food plant of *H   setariae*, which is much more
numerous on sugar cane and is therefore a longer period of time

Insect Motility—The motility of insects and their migration
habits are of considerable importance   Some insects, as the beet
leaf hopper, have definite periods of migration in which wide areas
of cultivated plants may become infested in a short period of

time   Other insect vectors spread slowly from centers of infestation and the diseases transmitted by them may be correspondingly slow in their spread   Aphids in certain stages of development are relatively inactive and move very slowly from plant to plant   The rate of spread of a virus disease by aphids may be increased by any cultivation practice that increases their motility   The practice of roguing virus-infected plants from a field may defeat its own purpose if the vectors feeding upon the diseased plants are allowed to move to the remaining plants Incomplete control of insect vectors by spraying or dusting may likewise hasten the spread of the disease by dispersing viruliferous insects from diseased to healthy plants

The prevailing winds or strong winds of some duration may influence greatly the incidence of a disease by its influence on the movement of the insect vectors   Wellman (1935) has shown that the spread of celery mosaic in Florida is dependent upon the movement of the aphid vector (*Aphis gossypii*) and that this is influenced greatly by the direction of the prevailing winds The winged forms of the vector may fly for a considerable distance and are responsible for new centers of infection, but their direction of flight is determined largely by the direction of the prevailing wind

Felt (1937) has studied the influence of the prevailing winds on the movement of the elm beetle (*Scolytus multistriatus* Marsh) and its significance in the spread of the Dutch elm disease in the United States   The study of wind drift by balloons in the regions infected with the Dutch elm disease indicates a drift in a northeasterly direction, which coincides very closely with the direction of greatest spread from the early centers of infection   Although no studies with the beetles have been made, there are several records of bark beetles being caught high in the air in airplane traps   Felt is of the opinion that "wind carriage of infected beetles affords the most reasonable explanation of the distribution of the Dutch elm disease in the northeast" and that balloon distribution data will indicate the general lines of further spread Fransen (1939) has observed that the elm bark beetles fly high above the treetops and that the taller trees are most frequently attacked whereas the lower ones escape

The migration habits of insect vectors should be studied more extensively than they have been in the past   Many vectors of

plant diseases feed for a time on certain species of wild plant, later migrating to the cultivated crops   The causes of migration may vary with different vectors   The beet leaf hopper apparently migrates from the native vegetation to the sugar-beet fields when the native vegetation dries up or matures with the approach of the hot, dry summer weather   Carter (1930) has shown, however, that the leaf hoppers migrate not alone because of the scarcity of food, but because they have an inherent instinct to migrate   This highly developed instinct probably evolved by natural selection in heterozygous populations, through the greater survival of those individuals with migrating instincts, as the native vegetation dried up year after year   The variability of the migration instinct and the time required for a change in migration habits are not known   If appreciable changes can be effected in a relatively few generations, the migration and food habits of insects could be modified strikingly by climatic cycles or by the changing agricultural practices of a region   Such changes would be of considerable significance in epiphytology and might explain the great fluctuation often observed in the prevalence of insect-transmitted diseases

Insects that are active and move from plant to plant frequently are more effective in transmitting viruses than the more sedentary species, other things being equal   This is a factor that should be kept in mind when evaluating the relative importance of different vectors   A very active species that is capable of transmitting a virus in only a small percentage of opportunities may be of greater importance than a more sedentary species that transmits the disease in a higher percentage of opportunities   Greenhouse experiments demonstrating that a given insect is capable of transmitting a virus should be supplemented by field studies of the habits of the insect before its role as a vector is finally evaluated

Tissue Selection —Many insects that feed upon a given plant do not do so indiscriminately   Nearly all species have a particular preference for certain tissues, and some are strictly limited in respect to the tissues on which they can feed successfully   This fact has a very important bearing on the subject of insect transmission of plant diseases   Slight differences in feeding habits and choice of tissues are often not noticed, and the significance of these differences is frequently overlooked until

revealed by careful and detailed study This aspect of the problem of insect transmission was greatly neglected for many years and still is in need of more careful study

The importance of tissue selection is strikingly illustrated by the investigations of Bennett (1934, 1937), Bennett and Esau (1936), and Fife and Frampton (1936) These workers have shown that the virus of curly top of beets is confined almost entirely to the phloem tissues of affected plants The virus is rarely found in the parenchyma tissue It was demonstrated also that the beet leaf hopper normally feeds on the phloem and that when viruliferous leaf hoppers feed only on tissues other than phloem they rarely, if ever, inoculate the plant with the virus There is, therefore, a close correlation between the tissue selection by the leaf hopper and its effectiveness as a vector of curly top

Fife and Frampton (1936) have offered the first plausible explanation of the method by which the leaf hopper is able to locate and select the phloem on which to feed This explanation is based on the existence of a pH gradient between the cell contents of the phloem and that of the parenchyma By using a potentiometer and a quinhydrone microelectrode to measure the acidity of the cell sap in various tissues, it was found that the sap of the phloem is considerably more alkaline than that of the surrounding parenchyma, resulting in a pH gradient as illustrated graphically in Fig 146 It was shown also that the reaction of the saliva of the leaf hopper is alkaline, approximating that of the liquids of the phloem These facts led to the hypothesis that the pH gradient was utilized by the leaf hoppers as a guide to the phloem According to this hypothesis, when the setae of the insect penetrate the parenchyma, the difference in acidity between the cell sap and the insect's saliva gives rise to an undesirable reaction, which causes the leaf hopper to withdraw or change the direction of its setae The process is continued with the result that the pH gradient leads to the phloem where the desired alkalinity is found

This hypothesis was supported by some additional experimental evidence Leaf hoppers were placed in artificial feeding cages where, by piercing a thin membrane, they could feed on drops of sugar solutions adjusted to two different pH values (pH 8 5 and pH 5 0) They were observed to explore the acid

drops with their setae and move on to the alkaline ones before
finally settling down to feed

The pH gradient normally found in beet-leaf tissue was modi-
fied by subjecting the beets to high concentrations of carbon
dioxide   This treatment tended to equalize the pH values of
the phloem and parenchyma as shown in Fig 147   When leaf
hoppers were fed on these treated beets, they were no longer able
to locate the phloem and fed indiscriminately on different tissues
with a corresponding decrease in effective inoculation with the
virus   These studies constitute an important contribution to
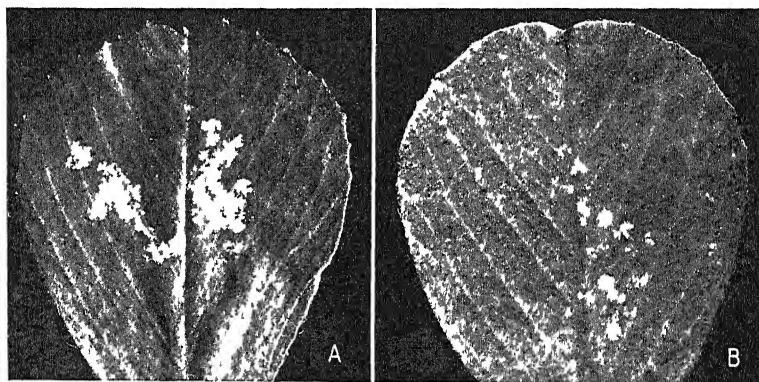
Fig 225 —Lesions made on alfalfa leaves by two species of *Empoasca* which do
not select the phloem on which to feed   *A*, a leaf fed upon by one adult of
Empoasca abrupta, B, by one adult of *E erigeron*   Approx $3\frac{1}{2} \times$ The stippling
effect is much less severe than the burning effect of *E fabae*   (*After Smith and
Poos*)

the study of insect transmission of viruses, and similar studies
should be made with other viruses and their vectors   A further
study of tissue selection by insects along with similar studies of
the localization of the viruses in plant tissues may explain many
cases of apparent specificity between certain virus diseases and
their insect vectors

There is some evidence that the ability of aphids to transmit
leaf roll of potato is associated with phloem feeding (Dykstra
and Whitaker 1938)   This virus is transmitted by several species
of aphid, but those which consistently feed upon the phloem
(*Myzus persicae, M circumflexus*, and *M solani*) transmit it
more readily than *Macrosiphum solanifolii* which feeds more
frequently on mesophyll tissues   On the other hand, the three

species of *Myzus* varied in their ability to transmit certain viruses of the potato although no differences in their feeding habits were observed

Tissue selection by piercing-sucking insects is significant, also, in the study of toxicogenic insects and the diseases caused by them   Smith and Poos (1931) have studied the tissue selection of six species of *Empoasca*   Five species (*E maligna, E abrupta, E filamenta, E bifurcata,* and *E engeron*) selected the mesophyll tissue of the more mature leaves upon which to feed   They caused only slight injury characterized by a spotting or stippling of the upper leaf surface (Fig 225)   In contrast, *E fabae* showed a decided preference for the phloem tissue   In feeding on the phloem, this species seriously disrupts the normal functions of the vascular elements, and the destructive pathological condition known as hopperburn then results

THE BREEDING HABITS OF INSECTS AS RELATED TO DISEASE TRANSMISSION

The effectiveness of an insect as a vector of a plant disease often may be influenced by its habits of breeding   Plant wounds made by insects in connection with breeding activities frequently serve as points of entrance for plant pathogens   The adults of some species tunnel into plant tissue and establish brood tunnels in which the eggs are deposited and the young are reared   The ambrosia beetles and the bark beetles breed in this way   Various kinds of fungi are usually associated with insects of this type, and in many cases the fungi are pathogenic to the plants in which the insects breed, *e g , Cerotostomella ips, Tuberculariella ips* causing the blue stain of conifers, and *C ulmi* causing the Dutch elm disease

The females of certain other species of insect are equipped with sharp-pointed ovipositors with which they make punctures in plant tissue for the insertion of their eggs   In general, this type of oviposition wound is not so important in the transmission of plant diseases as the one just described, but there are a few noteworthy examples of effective transmission through oviposition The female apple-maggot fly (*Rhagoletis pomonella* Walsh) inserts her eggs in punctures made with a sharp ovipositor in the tissues of apple fruit (Fig 93)   Pathogenic bacteria (*Phytomonas melophthora* Allen and Riker) are introduced along with the eggs

and eventually cause a decay of the apple (Allen, Pinckard, and Riker, 1934)   The olive fly (*Dacus oleae* Rossi) is said to inoculate olive twigs with the olive-knot pathogen [*Erwinia savastonoi* (Smith) Bergey *et al*] in a similar manner (Petri 1910) (Fig   90)

A unique example of inoculation at the time of oviposition is that of tree crickets and the canker of apples caused by *Leptosphaeria coniothyrium* (Fckl) Sacc as described by Gloyer and Fulton (1916)   The female tree crickets insert their eggs into punctures made with their ovipositors in the apple twigs   The punctures are then plugged with materials which often contain spores of the pathogen   Two species (*Oecanthus niveus* DeG and *O exclamationis* Davis) plug the puncture with pellets of chewed bark often obtained from cankers on which the fungus is fruiting   Other species use pellets of feces which also commonly contain viable spores of the fungus   The peculiar instincts manifested by these insects during oviposition are thus responsible for their importance as vectors of apple canker (Fig   128)

Many insects deposit their eggs on the surface of plant tissue without making wounds, but when the eggs hatch the larvae often bore into the tissues and inoculate them with plant pathogens The part of the plant on which the eggs are deposited may be significant in determining the amount of damage caused by the disease For example, the Dipterous insect vectors (*Scaptomyza graminum* Fall and *Elachiptera costata* Leow) of celery heart rot, caused by *Erwinia carotovora*, deposit their eggs on the surface of the celery leaves   In rainy weather, the eggs are deposited on the outer leaves, and the resulting soft rot is not very destructive   In dry weather, on the other hand, the insects seek a moist place to deposit their eggs and lay them on the young heart leaves near the growing point   When these eggs hatch and the larvae inoculate the heart leaves with the bacteria, the growing point is killed and much loss follows (Leach 1927)   The instinct that leads the insect to seek a moist place for depositing its eggs obviously greatly influences its significance as a vector

Most insects have decided preferences among the host plants on which they breed   Insect vectors often breed more abundantly on weeds and wild plants than they do on the economic plants on which they feed and to which they transmit diseases The control of many insect-transmitted diseases depends upon the destruction of the primary breeding hosts of the vector   For this reason, no study of an insect vector is complete until its

breeding habits, including its preference of breeding hosts, are accurately known. It has been determined that the plant bugs which transmit stigmatomycosis to cotton and other plants breed extensively on many weeds and noncultivated plants. Control measures for the disease depend largely upon keeping down the population of vectors through destruction of their weed hosts.

The breeding habits of insects in relation to cultural practices are also important from this standpoint. In the control of yellow top of alfalfa caused by the leaf hopper (*Empoasca fabae* Harris), it has been shown (Graber and Sprague 1933, 1935, Searls 1934, and Jewett 1934) that the population of hoppers and the subsequent injury can be greatly reduced by timing the first cutting to coincide with the end of the heaviest egg-laying period but to precede the hatching period. By doing this, the majority of the eggs of the first brood of hoppers is destroyed when the alfalfa is cut, and the second brood is so greatly diminished that it fails to cause much damage. The success of this method of control is greatly influenced by the weather conditions and the relationship between the stage of development of the insect and the growth stage of the alfalfa.

Insect Abundance —If a plant disease is largely dependent upon insects for its transmission, it is only reasonable to suppose that the prevalence of the disease will be influenced by the prevalence of its insect vector. This would be especially true of such diseases as bacterial wilt of cucurbits and certain virus diseases that are transmitted only by certain species of insect. A few observations have been recorded which indicate that such relationships exist. The influence would be less on diseases in which insects constitute only one of several agents of inoculation. It is a matter of common observation that the prevalence of both insects and plant diseases varies from year to year, but remarkably few studies have been reported in which the influence of fluctuating insect populations on the fluctuating prevalence of diseases has been considered. It is recognized that the populations of certain insect species fluctuate in definite cycles as a result of parasitism and other biotic factors. As the insect pest becomes more abundant, its parasites also may multiply. Soon the parasites kill so many of the host insects that the latter become relatively scarce. The scarcity of the host insect results in a diminishing of the population of parasites until the host insect again becomes more abundant and the cycle is repeated.

Cycles of this type have been recorded for a number of insect vectors, and there are numerous records of correlation between the prevalence of a vector and the disease that it transmits Plant pathologists, seeking to explain the variation in the prevalence of an insect-transmitted disease, should endeavor to learn as much as possible about the fluctuations in population of the insect vector and their possible relation to the fluctuations in prevalence of the disease

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CHAPTER XVI

INSECT TRANSMISSION OF ANIMAL DISEASES COMPARED WITH INSECT TRANSMISSION OF PLANT DISEASES

The sciences of plant and animal pathology have much in common   The phenomena dealt with are essentially the same, although the two sciences are cultivated by different groups of workers, each highly specialized in its own field   Each group is concerned with the fundamental biological processes of disease, *i e*, parasitism, pathogenicity, inoculation, infection, epidemiology, immunity, etc   A discovery made in one field often has direct application in the other and still more often may be the key to the solution of some vexing problem   Partly because of the higher values placed upon human lives, or the lives of animals, animal pathology developed somewhat earlier and has progressed more rapidly than plant pathology   Consequently, the younger science of plant pathology has in the past drawn much from the rich discoveries of medical science and may be expected to do so in the future   Therefore, a student interested in the subject of insects in relation to plant diseases will do well to acquaint himself with the known facts concerning the relation of insects to the spread and development of animal diseases

An exhaustive treatment of the subject of insects in relation to animal diseases is beyond the scope of this book   It will be sufficient here to give a brief historical account of the development of medical entomology and, for the purpose of comparison, to give the essential facts concerning a few representative examples of insect transmission of animal diseases   For further information on the subject, the reader is referred to the well-known works of Matheson (1932), Riley and Johannsen (1932), Fox (1925), and Wenyon (1926) and the literature cited by them

HISTORICAL

Interest in insects from the standpoint of their relation to the transmission of animal diseases is a relatively recent develop-

ment   The first general treatment of the subject was published in 1899 by Nuttal, who stated the situation at that time as follows "Very few of the works on hygiene even mention the role of insects as carriers of infection, and those that do generally speak vaguely on the subject" But since this statement was made, there has been a rapidly increasing interest in this aspect of entomology and medicine, and as new facts have been discovered, insects have proved to be a factor of prime importance in medical science   The past 40 years has witnessed the rapid development of the broad but specialized field of medical entomology

Despite what has been said, the idea of insect transmission of disease is not of recent origin   Various "theories" of insect transmission of human diseases date from the ancients   Experimental proof, however, was lacking, and the theories failed to influence scientific thought   With the first experimental proof of insect transmission, the theory became a fact, and the idea was rapidly exploited, stimulating further research in the field   With the exception of early inconclusive experiments dealing with insects and anthrax, the first experimental evidence that insects are concerned in the transmission of diseases is that published by Manson (1878, 1884) showing that mosquitoes are vectors of the filarial worm causing elephantiasis of man   Manson showed that the larvae of the parasite are taken up in large numbers by the mosquito when it sucks the blood of an infected person   He showed that the worm undergoes cyclic development in the body of the mosquito   Manson thought that the parasite was released in the water on the death of the mosquito and that man became infected by drinking contaminated water, but he was in error on this point   The true method of infection was discovered in 1900 by Low, who showed that infection followed the bite of an infected mosquito   The incompleteness of the work of Manson does not detract much from the significance of his contribution, for it influenced greatly the work of others and marked the beginning of medical entomology

The next great step forward was made by Smith and Kilbourne with their classic work on the cattle tick and the Texas fever of cattle, published in 1893   The tick, shown to be a vector of Texas fever, is not a true insect but a closely related arthropod   This work is of special historical significance because it marks the first proof of the transmission of a protozoal disease

by a bloodsucking arthropod   The recognition of this relationship and its significance in the epidemiology of animal diseases led to the discovery later of the vectors of the Rocky Mountain spotted fever of man, tularemia, and other similar diseases

A few years later (1895) Bruce, working in Africa, discovered that the fatal nagana disease of cattle is caused by a blood-inhabiting trypanosome and showed that the disease is conveyed from sick to healthy animals by the bloodsucking tsetse fly (*Glossina morsitans*)   This discovery paved the way for the demonstration of the cause and method of spread of the insidious and fatal African sleeping sickness of man, a disease very similar to the nagana disease of cattle   It is caused by *Trypanosoma gambiense* and is transmitted by several species of *Glossina*, or tsetse fly   Bruce and many other workers, including both entomologists and medical men, contributed to the solution of this problem

The next great advance, and one of much significance, was the proof of the transmission of malaria by mosquitoes   On the basis of observational evidence, many laymen as well as scientists had expressed the idea that mosquitoes were concerned in the spread of malaria, but in the absence of experimental evidence the theory had received little credence   As early as 1880, Lavaran had shown that malaria was caused by a parasitic protozoan and had suggested that it might be transmitted by mosquitoes   However, the major credit for experimental proof of the transmission belongs to Ross who, encouraged and inspired by Manson, worked out the development of the malarial parasite in the body of the mosquito   The publication of this work was soon followed by its confirmation and extension by many different investigators

A great impetus to research in this field and the most dramatic of them all was the proof of the transmission of yellow fever by the mosquito   This proof was supplied by the United States Army Commission headed by Walter Reed (1900), who was assisted by James Carroll, Jesse Lazear, and Aristides Agramonte   The significance of this discovery in the control of yellow fever is too well known to need repetition here   It is sufficient to say that it made possible the rapid suppression of one of the most dreaded diseases of mankind against which medical science previously had been entirely helpless   But this was not all

For once and all, it impressed upon the mind of scientist and laymen alike the importance of insects in the spread and development of diseases Entomology became an essential part of medical science

The last 35 years have seen a remarkable growth in the field of medical entomology Insects have been shown to play a vital part in the epidemiology of a dozen or more diseases of major importance affecting man or animal The story of the investigations leading to these discoveries is one of the most fascinating chapters in the history of medical science For the romantic and human interest side of the story, the student should read the books of DeKruif ("The Microbe Hunters," 1926), Howard ("Yellow Jack," 1933), and Kelley ("Walter Reed and Yellow Fever," 1906)

EXAMPLES OF ANIMAL DISEASES TRANSMITTED BY INSECTS AND RELATED ARTHROPODS

In order that we may have a basis for comparing the relation of insects to the spread and development of man and animals with similar phenomena in plant pathology, it will be necessary to consider a few representative animal diseases that are transmitted by insects They will be discussed primarily from the standpoint of insect transmission For more complete accounts of other aspects of the diseases, the reader must consult the standard medical texts The diseases will be considered also in the light of present-day knowledge, and it should be remembered that much information has been added since the work of the pioneers mentioned above

Mosquitoes and Filariasis —Filariasis is a disease of man caused by nematode worms that inhabit the blood and lymph A variety of symptoms are caused, one of the most common being enormous swellings on various parts of the body, the condition being known as "elephantiasis" The swellings are often accompanied by ulcers and other disorders arising from the stoppage of the lymphatic trunks The pathogen is a threadlike round worm (*Filaria bancrofti* Cobbold) The disease is indigenous in nearly all tropical and subtropical countries In the United States, it occurs in a small area around Charleston, S C

Transmission of Filariasis—Mosquitoes are the vectors of filariasis   Fifteen or more different species are known to transmit it, and no other method of spread in nature is known   The blood of man is the natural habitat of the filarial worm, and man is its definitive host, *i e*, the host in which the sexual stage of the parasite is found   Larvae occur in great abundance in the blood of affected individuals, as many as 600 being found in a single drop   The larvae, whose average size is about 8 by 300 microns, are sucked up with the blood by mosquitoes when they feed on

<div align="center">

a   *b*

</div>
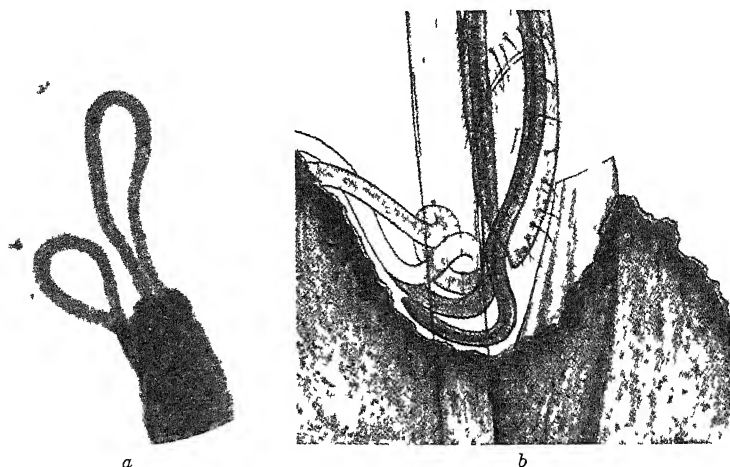
FIG 226 —Filaria larvae emerging from the labium of a mosquito   *a,* larvae emerging from labium of *Aedes variagatus, b,* a semidiagrammatic sketch showing larvae leaving labium of a feeding mosquito and burrowing into the skin   (*From Manson's " Tropical Diseases "*)

an infected individual   The larvae enter the stomach of the mosquito, escape from their sheath, bore through the intestinal wall, and migrate into the thoracic muscles   Here, in the course of 16 to 25 days, they undergo metamorphosis but do not increase in number   The mature larvae then migrate into the labium of the mosquito   The larvae, which are too large to pass through the food canal of the mouth parts, escape through the end of the labium when the mosquito feeds on a human being (Fig 226) On reaching the skin of the human host, they bore through it and enter the blood stream   Thus, the larvae are not introduced into the blood by the mosquito, they bore through the skin by their own power   Upon reaching the lymphatics,

the worms become sexually mature, fecundation occurs, and the females give birth viviparously to enormous numbers of larvae The new crop of larvae enters the blood stream, thus completing the cycle

It should be noted that both man and mosquito are necessary for the completion of the life cycle of the parasite Man is the definitive host, the mosquito is the intermediate host Since the pathogen is not injected by the feeding punctures of the mosquito but penetrates the skin by its own power, infection is contaminative

Cattle Ticks and Texas Fever —Texas fever, or red-water fever, is a widely distributed disease of cattle It is characterized by a high temperature and a destruction of the red blood corpuscles with the consequent red discoloration of the urine It is usually fatal although light attacks are not uncommon It has been one of the most destructive diseases of cattle throughout the southern part of the United States, and the same or a closely related disease is known to occur in other parts of the world

The disease is caused by a minute protozoan parasite of the red blood corpuscles (*Babesia bigemina*)

Transmission of Texas Fever —Ticks are responsible for the transmission of Texas fever No other method of spread in nature is known, although several different species of ticks may serve as vectors [*Boophilus annulatus* (Fig 227), *B dugesii, B discoloratus*, and *Ixodes ricinus*] When the tick feeds upon infected cattle, it ingests the pathogen along with the blood The pathogen undergoes a complicated sexual reproduction and multiplies in the body of the tick, large numbers of individuals of a specialized form being thus produced The new forms of the pathogen enter the ovaries, invade the eggs, and infect the young "seed" ticks before they are born, eventually finding their way into the salivary glands of the new generation The mature female ticks fall from the infected cattle and deposit their eggs on the ground The eggs soon hatch, and the young ticks crawl up on blades of grass from which they succeed in getting onto new cattle When the ticks feed on the cattle, the parasites pass from the salivary glands of the ticks into the blood of the cattle where they infect the red blood corpuscles

It should be noted that the tick is the definitive host and the cow is the intermediate host Both the tick and the cow are

necessary for the completion of the life cycle of the parasite
Infection is inoculative, the pathogen being introduced into the
blood through the feeding punctures of the vector   The parasite
is transmitted congenitally through the egg of the vector, and
the disease is not transmitted by the same tick that feeds on the
infected cow but by its progeny   Thus, two generations of the
vector are necessary for the completion of the transmission cycle

A   B

FIG 227 —The cattle tick (*Boaphilus annulatus*), the vector of Texas fever
A, engorged female, *B*, liberation of eggs   (*Photograph reproduced by courtesy
of Bur Animal Indus U S Department Agriculture*)

The Tsetse Fly and the Nagana Disease of Cattle.—The
nagana disease is very destructive to cattle in Africa   The
hair falls out of affected animals, and the flesh wastes away
There is a running of the nose and mouth accompanied by watery
blisters   Blindness eventually develops, and the disease is
nearly always fatal   The nagana disease is found only in Africa
in regions where the tsetse fly is present   The cause of the
nagana disease is a trypanosome (*Trypanosoma brucei*)

Transmission of the Nagana Disease —This disease is transmitted in nature exclusively by the tsetse fly, *Glossina morsitans* (Fig 228) although it may be transmitted experimentally by artificially inoculating animals with the blood of an infected animal   The trypanosomes are sucked from the blood stream of affected animals by the fly and, in the body of the insect, undergo a sexual developmental stage requiring a minimum of 10 days   During this 10-day period, the fly is not infective, but after the incubation period is completed the fly remains infective for a long time   The pathogen may be found in the blood of many wild animals that show no marked symptoms of
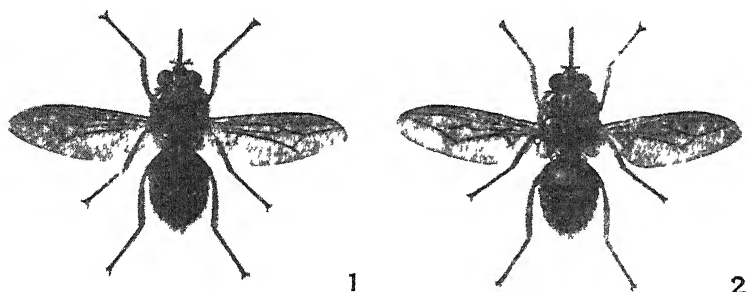
Fig 228 —Tsetse flies, the vectors of sleeping sickness   1, *Glossina palpalis*, 2, *G morsitans*   (*From Manson's " Tropical Diseases "*)

the disease   These serve as reservoirs from which the pathogen is transmitted to the domesticated cattle

The insect vector in this case is the definitive host, and the cow is the intermediate host serving as an intermediate host reservoir   Infection is inoculative, the pathogen being introduced directly into the blood stream by the biting fly   The pathogen is not congenitally transmitted in the vector, each insect acquiring it by sucking the blood of an infected animal

The Tsetse Fly and Sleeping Sickness —A disease of man very similar to the nagana disease of cattle occurs in many places in Africa   It is indigenous to Africa and has been present for a long time, but, with the development of commerce and travel, it has become more widespread and destructive   The disease is slow and insidious, being practically always fatal   It is characterized by dullness, apathy, and eventually complete lethargy, symptoms that are responsible for the name "sleeping

sickness " The flagellate *Trypanosoma gambiense* is the casual agent (Fig 229)

Transmission of Sleeping Sickness —Like the nagana disease, sleeping sickness is transmitted by several species of tsetse fly, principally *Glossina palpalis* (Fig 228) and *G tachinoides* The life history of the parasite, its method of transmission and its host relationships, in all essential respects, are comparable to those of the nagana disease

Efforts to control the sleeping sickness have emphasized strikingly the importance of a complete knowledge of all aspects of the
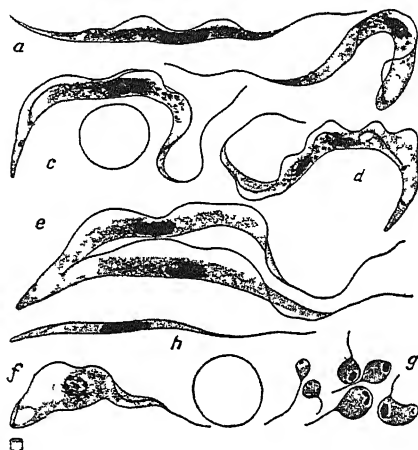
Fig 229 —*Trypanosoma gambiense*, the cause of African sleeping sickness and transmitted by *Glossina palpalis* Various forms from the blood and cerebrospinal fluid   (*From Manson's 'Tropical Diseases'*)

transmission of a disease   With more complete knowledge of the insect vectors, their habits, and geographical distribution, many early conclusions have proved untenable   The most insignificant detail in the life history and biology of the vectors becomes of prime importance in fighting the disease   The marked success that has been attained has resulted from close cooperation between the entomologists and the physicians in their investigations of all aspects of the disease and its insect vectors   A graphic statement of some of the problems involved and how they are being solved has been given by Swynnerton (1936)   There are 21 known species of *Glossina* indigenous to Africa, each requiring different vegetative and animal ecology for their opti-

mum development Remarkable control of the insects and sleeping sickness has been accomplished through ecological modification of the infested areas The use of properly designed clearings and of plant barriers, especially evergreen barriers, has been very effective The combined efforts of entomologists zoologists, botanists, and physicians have been largely responsible for the success attained

Mosquitoes and Malaria —Malaria is said to be the worst scourge of mankind It is one of the most widely distributed
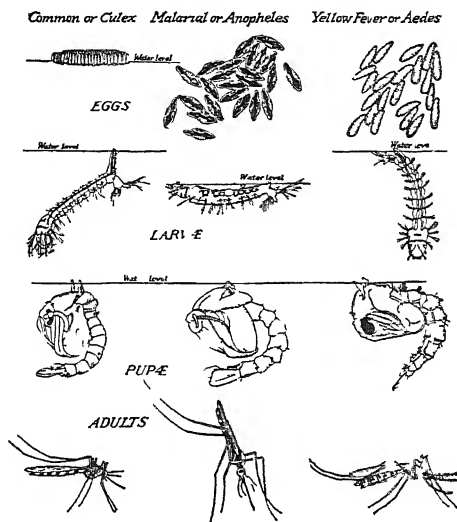
FIG 230 —The life stages of three types of mosquitoes, *Culex, Anopheles* and *Aedes* The latter two types are vectors of malaria and yellow fever, respectively (*From "Everyday Problems in Science," Pieper and Beauchamp copyrighted by Scott Foresman & Company, after Metcalf and Flint*)

diseases affecting man, occurring throughout the tropical and subtropical regions of the world It is not so fatal as certain other diseases, but its debilitating effect on such a high percentage of the population makes it a serious factor in the health of man The characteristic symptoms of malaria are intermittent "chills" followed by fever and a chronic languor and debility

Malaria is caused by minute protozoa that invade and destroy the red blood corpuscles Three different species are recognized, each causing a distinct type of malaria (1) *Plasmodium vivax*, causing tertian, or benign, malaria, (2) *P malariae*, causing quartan malaria, and (3) *P falciparum*, causing malignant or

estivo-autumnal malaria   The benign, or tertian, malaria is the most prevalent type in North America

Transmission of Malaria —Mosquitoes of the genus *Anopheles* (Fig 230) are the only known agents of transmission of malaria The common *Culex* mosquito is not a vector   Many different species may transmit the disease, but not all of them transmit it with the same degree of effectiveness   The relation of the mos-
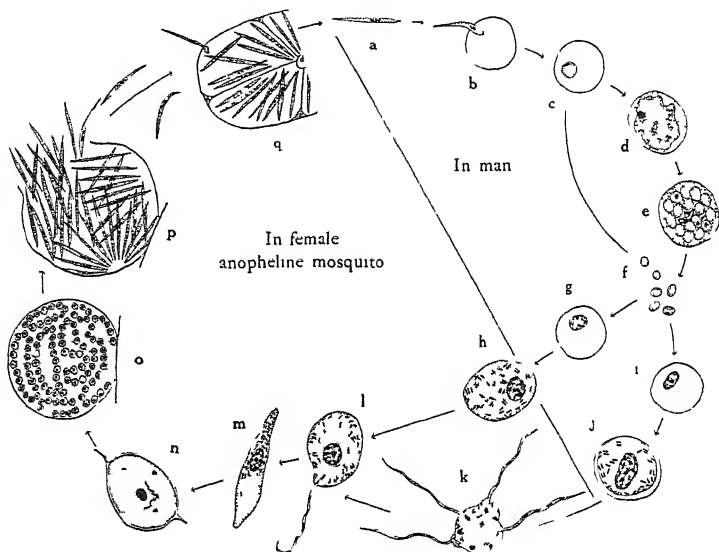
Fig 231 —The life cycle of the malarial pathogen in man and mosquito illustrated diagrammatically   The sporozoites are introduced into the blood of man from the salivary glands of the mosquito (*a*)   In the human blood stream the parasite multiplies asexually (*c* to *f*) forming micro- and macrogametocytes (*g* to *j*)   When the patient is bitten by a mosquito, these are taken into the body of the insect where the parasite multiplies sexually (*o* to *p*), the salivary glands becoming charged with sporozoites (*q*) completing the cycle   (*After Kudo ' Protozoology," second edition, by permission of Charles C Thomas publisher)*

quito to malaria has been studied extensively and constitutes what is perhaps the best-known example of insect transmission of a disease   The life history of the pathogen in the human body and in the mosquito has been worked out in great detail and is described adequately in many standard texts   The relationship of the mosquito and *Plasmodium vivax* is, briefly, as follows In the blood of the human body, the plasmodium inhabits the red corpuscles where it multiplies asexually, causing the cell to

swell and burst, liberating from 15 to 24 *merozoites*, each of which attacks a new red cell and repeats the process in about 48 hours After several days of asexual multiplication, male and female cells (*micro-* and *macrogametocytes*) are formed   No further change in the life cycle of the pathogen takes place in the human body, the mosquito being essential for further development When an infected person is bitten by an anopheline mosquito, the sex cells of the pathogen are ingested with the blood (Fig 231) Fertilization takes place in the stomach of the mosquito, forming a *zygote*   The zygote, or *ookinete*, penetrates the wall of the mosquito's stomach, where it enlarges and transforms into an *oocyst*   After a time, the enlarged oocyst bursts and liberates into the body cavity a large number of minute *sporozoites* which invade the salivary glands and are ready to be injected into the blood stream of the next victim that the mosquito bites   The incubation period, or the time required for the completion of the cycle in the insect, is 8 to 14 days   The pathogen may live for several months in the mosquito but does not usually survive the winter in the insect's body, although such survival is possible The gametocytes may survive for long periods of time in the blood of man, even though they may not cause active symptoms of malaria   Individuals that harbor the gametocytes but have no active symptoms are called "carriers" and are important sources of infection   Birds and other animals are subject to malaria caused by similar but different species of the parasite They are not intermediate host reservoirs for the malaria that affects man

Mosquitoes and Yellow Fever —Yellow fever is among the most virulent diseases of man and has been one of the most dreaded of all epidemic diseases   It is acute and noncontagious, causing prostration, jaundice, and hemorrhages, and the percentage of fatalities is high   The disease was very prevalent for many years in the areas bordering on the Caribbean Sea, and although it was known to occur in other parts of the world, it was generally considered to be of American origin   It was recognized as a disease of civilized regions, apparently being transmitted only by the domestic mosquito [*Aedes aegypti* (L)], but with the discovery of endemic yellow fever among the natives of Central Africa and South America, in the absence of *A aegypti*, the whole question was reopened (Carter 1931, Shannon, Whit-

man and Fianca 1938)   Yellow fevei is caused by a filterable virus

Transmission of Yellow Fever —Yellow fevei, like malaria, is tiansmitted only by mosquitoes   No othei method of tiansmission is known   Foi a long time after the first demonstration of mosquito transmission by Reed and his associates in 1900, it was believed that only one species (*Aedes aegypti*) (Fig 230) was capable of transmitting it   Expeimental woik on transmission was long handicapped by the absence of any known hosts othei than man   In 1928, Stokes, Bauei, and Hudson showed that certain monkeys were susceptible to yellow fever, and with the aid of this new expeimental animal Bauer (1928), Shannon, Whitman, and Franca (1938) and others soon demonstiated that mosquitoes other than *A   aegypti* are effective vectors   Now it is known that a dozen oi moie different species may transmit the virus   Many of these are species inhabiting the jungles, and the viius has been demonstrated in mosquitoes caught in theii native jungle habitat

The incubation period of yellow fevei in man is 3 to 7 days   The work of Reed and his associates indicated that in oidei to transmit the virus the mosquito must feed upon an infected man during the first 3 oi 4 days after the initial symptoms of the disease   In monkeys, however, the virus persists in the blood stream throughout the course of the disease and may be acquiied by the mosquitoes at any time   An incubation period of 9 to 14 days in the mosquito is iequired befoie the viius can be transmitted   The nature of this incubation peiiod and what changes, if any, occur in the virus aie not known   After the incubation peiiod, the mosquito is capable of transmitting the viius as long as it lives   A single bite of one infected mosquito is sufficient to produce infection   Although congenital transmission of the virus in the mosquito has been claimed by some workers, the more recent evidence has failed to support the claim

As soon as it was leained that yellow fevei was transmitted by mosquitoes, efforts were made to control the disease by exterminating the mosquitoes   So successful weie these efforts that the disease practically has been eliminated fiom the moie civilized regions of America   Equally successful iesults were obtained in the Philippine Islands, but only after a careful study was made of the habits of the mosquitoes responsible for its spiead   The

active vector in the Philippines has breeding habits so different from those of *A aegypti* that the measures used in Cuba and Panama would not have been effective   In fact, the breeding habits of the different species vary widely, and the control of yellow fever in any region must be based largely on a complete knowledge of the life history and breeding habits of all the mosquitoes capable of transmitting the virus

Mosquitoes and Dengue —Dengue, or breakbone fever, is prevalent throughout many tropical and subtropical regions of the world   It is characterized by headache and severe body and limb pains but is rarely even fatal   It is infectious and often occurs in epidemic proportions   There was a severe epidemic in Texas and neighboring states in 1922   The cause of the disease is not known definitely, but the infectious agent has many of the characteristics of a virus

Transmission of Dengue —Dengue is transmitted by mosquitoes, the most important species being *Aedes aegypti* and *A albopictus*   The method of transmission is similar to that of yellow fever in all essential respects   The virus appears to be in the blood stream and can be acquired by the mosquitoes only during the first 3 days of the attack   An incubation period of 8 to 11 days in the mosquito is necessary before transmission is possible   The mosquito retains the virus for the length of its life, but there is no evidence of congenital transmission by the mosquito   Monkeys are susceptible but show no clinical symptoms, although they may serve as animal reservoirs

Fleas and Bubonic Plague.—Bubonic plague is an acute infectious disease affecting both man and rodents   It is a bacterial disease caused by *Pasteurella pestis* (Lehman and Neuman) Bergey *et al*   In man, it is characterized by swellings of the lymphatic glands, usually on the neck, armpits, or groins, often accompanied by black spots or blotches under the skin   There is sometimes a secondary congestion of the lungs causing the so-called "pneumonic" form of the disease   Plague is highly fatal to both man and rodents   It is the Black Death of the Middle Ages and was the cause of the Great Plague of London in the seventeenth century   The devastating nature of its epidemics made it one of the most dreaded of the diseases of man

Transmission of the Plague —Plague is primarily a disease of rodents, rats, mice, ground squirrels, and many other species are

affected   It may be transmitted by direct inoculation, but in
nature the principal agents of transmission are fleas   Any flea
that feeds upon both rodents and man may transmit the disease
to man, and most of the fleas that feed upon rodents will, under
certain conditions, feed on man   Man is most frequently
affected when rats die of plague and the fleas leave the dead rats
and infest man   Because of the life habits of rats which infest
human habitations, they are the most dangerous of the rodents
in spreading the disease among man   The black rat (*Rattus
rattus*) and the brown rat (*Rattus norvegicus*) are species most
concerned   More than a dozen species of fleas may transmit
plague, but the Indian rat flea (*Xenopsylla cheopsis*) is the most
universally important one

The flea is not a true intermediate host for the plague bacteria,
for no cyclic development occurs within its body   Therefore, it
is not the only possible agent of transmission   Artificial direct
inoculation is effective, and the disease can be transmitted by any
agency that is capable of introducing the bacteria into the blood
However, in nature the rat flea is the most effective vector and
the only one of any great significance

The bacteria multiply in the bodies of the fleas that have fed
on infected rats   The bacteria may pass through the intestinal
tract in a viable condition, contaminate the skin, and gain
entrance through wounds made by scratching   The bacteria
also may be inoculated directly under the skin in the feeding
process by certain individual fleas in which the stomach opening
is clogged so that blood and bacteria are regurgitated and forced
back into the feeding wounds   Transmission, therefore, may be
either contaminative or inoculative

The control of plague is based upon the destruction of the rat
and its fleas   The disease is commonly spread to new regions by
rats carried on ships, the infected rats leaving the ship and start-
ing an epidemic on shore   Ships from infected ports are fumi-
gated not to kill the germs directly but to kill the rats and their
fleas   Control by this means has been very successful in the more
civilized countries, but in some of the less advanced tropical
countries the disease still persists   Also, where the native wild
rodents have become infected they serve as potential reservoirs
from which the disease may spread to the semidomesticated rats
and from them to man

Lice and Typhus Fever —Typhus fever is a disease of ancient origin and of wide distribution   It is most prevalent in temperate and cold climates and is closely associated with crowded and unsanitary living conditions   It is usually prevalent among armies in wartime   The mortality varies from 5 to 50 per cent Typhus fever is caused by *Rickettsia prowazekii*, a minute intracellular microorganism found in the epithelium of the intestines of lice as well as in the blood of man when affected with the disease

Transmission of Typhus Fever —Lice (*Pediculus humanus*) are the agents of typhus transmission, the disease having been transmitted experimentally by lice from monkey to monkey No other insect vector is known   There is a required incubation period of 8 to 9 days in the louse before it can transmit the disease   Transmission may be inoculative through the feeding punctures of infected lice, or contaminative by infected excreta of infected lice, the pathogen entering through abrasions in the skin such as those made when the infested person scratches himself   The crushed bodies of infected lice also may serve as a source of inoculum   There are some indications that the pathogen may be congenitally transmitted in the louse, but the evidence is not conclusive

Lice and Trench Fever —Trench fever is a disease similar in many respects to typhus fever, but much less fatal   It was prevalent among the soldiers of the World War and was first recognized as a distinct disease at that time   It is caused by *Rickettsia quintana,* a microorganism found consistently in the stomach of infected lice

Transmission of Trench Fever —Trench fever is infectious and may be transmitted by artificial inoculation but in nature is transmitted almost exclusively by lice (*Pediculus humanus*) Transmission may be inoculative, the pathogen being introduced into the blood through the feeding of infected lice, or contaminative through the excreta of lice coming in contact with abrasions in the skin   An incubation period of 5 to 9 days in the lice is necessary before transmission is possible by either means   The pathogen is not congenitally transmitted through the eggs of the lice

Flies and Typhoid Fever —Typhoid fever is an enteric infection caused by *Eberthella typhosa* (Zopf) Weldin   The pathogen is

primarily a parasite and does not survive very long outside of the human body, but it may survive long enough to be transmitted through food and drinking water   It is found principally in the intestines, urinary bladder, gall bladder, and blood stream   The bacteria are voided in great numbers in the excrement and urine of affected individuals   Infection follows ingestion of the bacteria, which occurs most frequently as a result of using contaminated food or drinking water

Transmission of Typhoid Fever —Because of the method of infection and the prevalence of the pathogen in the excretory products of typhoid patients, the transmission of typhoid fever is accomplished largely by the contamination of food and drink with bacteria from exposed excrement or untreated sewage   This contamination may be brought about in several ways   One of the most common is through direct contamination of the water supply from fresh excrement or sewage, another common method is by direct contamination of food or milk through handling by a· chronic carrier, a person who has recovered from typhoid fever but continues to pass the pathogenic bacteria in the feces or urine   Fortunately only a small percentage of recovered patients are carriers   The common housefly (*Musca domestica* L) also has been incriminated as a vector of the typhoid bacillus   Houseflies are common inhabitants of sewage and exposed human feces, they not only walk over the contaminated material but feed upon it and ingest the bacteria, they also breed in contaminated material and are common visitors to exposed food and milk   It has been demonstrated that the typhoid bacteria may survive within the puparia of the housefly (Bacot 1911) but in view of the abundant opportunity for contamination in other ways it is not known how important this fact is in the epidemiology of the disease   Its chief significance would probably be in preserving the bacteria over an unfavorable period

The housefly, in addition to being a vector of typhoid fever, has been incriminated along with closely related species as a vector of a number of other animal diseases   In all cases, the method of transmission is essentially the same, infection being contaminative and resulting from the pathogen borne either eternally or internally by the vector   In the latter case, the contamination follows regurgitation or defecation

A BRIEF COMPARISON OF INSECT TRANSMISSION OF PLANT AND ANIMAL DISEASES

The foregoing examples are fairly representative of the most important insect-transmitted diseases of animals and offer a basis for comparison with insect-transmitted plant diseases   To facilitate the comparison, a tabular summary of the phenomena of insect transmission, as represented by these diseases, is given in the appendix, along with similar tables for representative insect-transmitted plant diseases   It will be noted that there are many striking similarities in the phenomena associated with insect transmission of the two kinds of disease   There are also a number of significant differences   In general, the same kinds of pathogen are involved in both groups of insect-transmitted diseases   The virus diseases constitute the largest group of insect-transmitted plant diseases, followed by the fungus and bacterial diseases, with only a few caused by protozoa   Diseases caused by protozoa lead the list of insect-transmitted animal diseases, followed closely by *Rickettsia* and viruses and a smaller number of bacterial diseases   There appear to be no fungus diseases of animals that are transmitted to any extent by insects

There is a wide variation in the specificity of the relationships between vector and disease in both groups   In plants, the more highly specialized relationships are found in the virus diseases which are, for the most part, transmitted by the sucking insects   Similar specialized relationships are found in the virus diseases of animals and in many animal diseases caused by protozoa that are transmitted only by certain bloodsucking insects   The highest degree of specialization is found in the latter group where the insect vector is often a definitive host and is necessary for the completion of the life cycle of the pathogen   Although there are several plant diseases in which the insect vector is obligatory, the definitive-host relationship is not known, with the possible exception of one or two incompletely studied cases among the endophytic protozoa   As an example may be mentioned *Phytomonas davidi* causing a flagellosis of *Euphorbia*   This phytopathogenic flagellate is transmitted by *Stenocephalus agilis* which Franca (1920a) claims is a definitive host, having seen what he interpreted as a sexual stage of the flagellate in the insect

In so far as is known, animal diseases, such as typhus fever and trench fever, are transmitted in nature by a single species of insect   Among plant diseases, the curly top of sugar beet peach yellows, cranberry false blossom, and a few other virus diseases are each transmitted by a single species of insect

Malaria is transmitted only by mosquitoes of the genus *Anopheles* whereas yellow fever is transmitted by several genera of mosquitoes   Similar examples of group specificity are found among the plant diseases as represented by corn streak, transmitted by three species of *Cicadulina,* and by potato leaf roll, transmitted by several genera of aphids

The necessity for an incubation period in the body of the insect vector is a phenomenon common to transmission of both plant and animal diseases   In the case of protozoal pathogens where a cyclic development is known, the nature of the incubation period is obvious, but the nature of the incubation period in vectors of virus diseases of both plants and animals is not definitely known

Congenital transmission of the pathogen occurs in vectors of both plant and animal diseases but is not a common phenomenon in either group   The protozoal pathogen of Texas fever is congenitally transmitted by the cattle tick, and the virus of the dwarf disease of rice is transmitted in a similar manner to successive generations of the leaf hopper (*Nephotellix apicalis*)

In reference to both plant and animal diseases, a knowledge of the phenomena of insect transmission has aided greatly in the control of the diseases concerned   The limits of possible control, however, have not been reached   There is much yet to be gained through more extensive studies of insect transmission of plant diseases, and those who investigate the field will profit greatly by acquainting themselves with what has been accomplished in the study of insect transmission of animal diseases

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CHAPTER XVII

METHODS OF INVESTIGATING THE RELATION OF INSECTS TO THE SPREAD AND DEVELOPMENT OF PLANT DISEASES

Research in the field of insect transmission of plant diseases does not differ from that in any other field of biology in so far as the basic principles are concerned   The same general procedures are necessary   Observation, experimentation, analysis and interpretation of data, constructive imagination for the building of working hypotheses, and inference, both deductive and inductive, are all essential   The technical methods involved, however, are unique in that they embrace those of two distinctly different fields of research, namely, phytopathology and entomology   Workers in each of these two fields have developed a series of technical methods particularly adapted to their needs, and each group of workers is relatively unfamiliar with the techniques of the other group   Few workers trained primarily as plant pathologists have had much experience in handling and rearing insects   The average entomologist likewise has had little experience with the bacteriological and mycological techniques that are basic necessities in the study of plant diseases   The lack of familiarity with either type of technique is a great hindrance in the study of insect-transmission problems and often discourages an investigator from doing work in the field

The investigation of problems in insect transmission of plant diseases is often done cooperatively by one or more workers from each field   This is desirable because of the added experience and knowledge of techniques brought to bear on the problem   Theoretically, the problem of techniques could be solved by cooperation in which the work requiring entomological technique would be done by the entomologist and that requiring phytopathological technique by the phytopathologist   In practice, however, such strict division of labor is rarely successful   Cooperative research organized on this basis often is little more

than regimentation, and when research is regimented the spirit of adventure is lost   Experience has shown that regimented research is rarely, if ever, productive research   It is sometimes stated that among social insects, such as bees, ants, and termites, the welfare and personal interests of the individual are completely subordinated to the welfare of the group and that a similar social organization should be striven for in human endeavors   This stage of social development, however, has not been reached in human society, and complete subordination of personal interest is not found often in cooperative research   Because of the personal equation involved, a less highly socialized and more flexible plan of cooperation is more likely to be successful   Moreover, it is frequently impossible to make sharp divisions of the work on the basis of technique   More often than not, the two kinds of technique and the problems being investigated are so closely interrelated that no practical division is possible

It is beyond the scope of this book to present an extensive discussion of the techniques of plant pathological and entomological research   In this chapter, certain general principles peculiar to the problem of insect transmission will be discussed briefly, and a few items of technique that are directly applicable to the subject will be described   The principles and techniques of research in plant pathology have been treated by Riker and Riker (1936) and Rawlins (1933), and Peterson (1934, 1937) has published well-illustrated manuals of entomological equipment and methods   These publications will be found very helpful by the student of insect transmission of plant diseases

KOCH'S POSTULATES

Before a satisfactory study of insect transmission of a plant disease can be made, it is necessary to learn as much as possible about the nature and cause of the disease that is transmitted   If the disease is caused by a microorganism, it is highly desirable that the nature and identity of the organism be known and its pathogenicity proved beyond doubt   In the last quarter of the nineteenth century, shortly after the discovery that bacteria could cause animal diseases, many species of bacteria were reported as causing disease but adequate proof of pathogenicity was often lacking   In an effort to discourage this practice, Koch (1883) published a statement of certain requirements

that he thought should be met before a claim of pathogenicity
is made   These requirements have been accepted in principle
by both animal and plant pathologists   They are generally
known as "Koch's postulates"   Every investigator who works
with insect transmission of a disease should be familiar with them
They may be stated briefly as follows

1   It must be demonstrated that the microorganism occurs consistently
associated with the disease in question
2   The microorganism must be isolated in pure culture and adequately
described
3   The disease, with characteristic symptoms, must be reproduced by
artificial inoculation of a suitable suscept with the microorganism in pure
culture
4   The microorganism must be reisolated from the inoculated suscept
and identified with the one used for inoculation

Obviously, it has not been possible to apply these postulates
to those diseases caused by obligate parasites and by virus
diseases, for no technique for growing these pathogens in artificial
culture is known   Other criteria of proof must be used for such
diseases   The relation of Koch's postulates to virus diseases,
with particular reference to animal diseases, has been discussed
by Rivers (1937), who points out that the spirit of the postulates
can be met even though the virus cannot be cultivated in artificial
media

Complete proof, in the spirit of Koch's postulates, that a virus
is the cause of a plant disease would require the demonstration
of the following facts

1   That inoculum taken from the diseased plant and freed from ordinary
microbes by filtration or other means will cause the disease when inoculated
into healthy plants
2   That the infectious agent was neither fortuitously present in the inocu-
lated plant nor introduced from some extraneous source (this can be demon-
strated by adequate checks in the inoculation experiments)

If the disease is transmitted by insects and not by artificial
sap inoculation, complete compliance will require transmission
by feeding the insect vector on filtered extracts from the diseased
plants and subsequently letting it feed upon healthy plants
Methods useful for this have been described by Carter (1927,
1928), Severin and Swezy (1928), Storey (1932), Bennett (1935),

Bennett and Esau (1936), and others   Several different types of insect cage adapted to feeding the insects on filtered plant extracts have been used   All make use of a thin membrane which separates the liquid from the insects and through which the insects feed   The feeding cage used by Storey (1932) in feeding the leaf hopper (*Cicadulina mbila*) on filtered extract from corn affected with streak is shown in section in Fig 232 The membrane used is that known as "Baudruche capping skin" and has proved to be very satisfactory for this purpose   The filtered juices are placed in the upper section and the leaf hoppers in the lower   The cage is set up so that the strongest source of light for the hoppers is seen through the membrane   By virtue of the light, the insects are attracted to the membrane, through which they feed upon the drops of filtered extract   The cages used by Bennett (1935) for feeding the sugar-beet leaf hopper on extracts from beets affected with curly top are of similar construction, but the insects were placed in the upper chamber and drops of the liquid were placed on the underside of the membrane   Other modifications of this feeding cage have been described by Hamilton (1930)   Fife (1932) has devised a method in which paraffin sections cut 60 microns thick are substituted for the usual membrane   When small drops of liquid

Fig 232 —A convenient feeding cage for feeding-sucking insects on filtered plant extracts or other solutions   *a*, Glass tube containing the feeding fluid, *b* membrane of Baudruche capping membrane, *c*, rubber stopper *d*, glass tube 8 inches long and 1 inch in diameter in which the insects are caged   *e* muslin cover, *f*, rubber band   (*After Storey*)

are placed on the paraffin, the insects (*Eutettix tenellus*) readily penetrated the thin slice of paraffin and fed upon the liquid

By virtue of the small drops of liquid used, this method was valuable in determining the pH of the salivary secretions of the insect and optimum pH of artificial nutrient solutions

The liquid used by Storey for feeding the leaf hoppers was prepared by crushing diseased corn plants and squeezing out the juice, filtering it first through paper pulp, and mixing the filtrate with an equal part of a 20 per cent sucrose solution This fluid was then mixed with a suspension of test bacteria and filtered through Chamberlain and Berkfeld filters   The filtrates were tested for sterility and then used for feeding the leaf hoppers, which, after feeding on the liquid for 24 hours, acquired the virus and transmitted the disease to healthy plants by feeding   This method is not only valuable for proving the filterability of viruses that are transmitted solely by insects but is useful also in the study of other aspects of the problem   The method has been used by Bennett (1935) and Bennett and Esau (1936) in studies of the properties of the curly-top virus and the movement of the virus in the plant   In these studies, an improved technique of preparing extracts for use in feeding the leaf hopper was devised

Juice was expressed from the tissues to be tested and added to an equal volume of 95-per cent alcohol   The resulting precipitate was thrown down by centrifugation, washed once with 50-per cent alcohol, dried, mixed with a volume of 5-per cent sugar solution equal to the original volume of juice, and centrifuged, and the supernatant liquid was used to feed non-viruliferous leaf hoppers

The more recent work of Vinson and Petre (1929, 1931), Stanley (1936a, 1936b), Thornberry (1938), Vinson, McReynolds, and Gingrich (1939), and others, in which techniques have been devised for isolating virus proteins in crystalline form, may provide a more direct way of meeting the requirements for proof that diseases are caused by viruses   The techniques for isolating the virus proteins have not yet been standardized adequately, and continued study will doubtless result in many refinements over the ones in use at the present time   The original method used by Stanley (1936a), who first isolated the virus protein in crystalline form, was soon modified and improved so that the yield of crystalline protein was practically doubled (Stanley 1936b)   The original method consisted in the precipitation with ammonium sulphate of the globulin fraction from a dilute

disodium phosphate extract of frozen, macerated, infected plants, and the removal of the coloring material by treatment with lead subacetate and celite   In the improved method, lead subacetate is not used, the precipitation and clearing being accomplished with ammonium sulphate, celite, and calcium oxide   The essential steps in the method are as follows (Stanley 1936*b*)

Tobacco plants affected with mosaic are cut, frozen, and put through a meat grinder, and the pulp is extracted twice in a fruit press with 0 1 m sodium phosphate at pH 7   The two extracts, each of which should equal about 70 per cent of the volume of the original pulp, are combined, and ammonium sulphate is added at the rate of 300 grams to 1,000 cubic centimeters of extract   The precipitated globulin is collected by gravity filtration through paper and when analyzed should yield almost 2 grams of protein to each 1,000 cubic centimeters of original extract   The precipitate is dissolved in 0 1 m sodium phosphate solution at pH 7 and filtered, with suction through a thin (0 5 centimeter) layer of celite (Hyflo Standardcel) on a Buchner funnel   The celite filter cake is washed with 0 1 m sodium phosphate at pH 7, and the protein in the filtrate is precipitated with ammonium sulphate, added at the rate of 20 grams to 100 cubic centimeters of filtrate   The precipitated protein is collected on filter paper and dissolved in 0 1 m sodium phosphate at pH 7   About 8 to 11 per cent by weight of ammonium sulphate is added, producing a slightly turbid solution which is filtered through a thin layer of celite, with suction, on a Buchner funnel   The celite filter cake is washed with 8 per cent ammonium sulphate solution and this filtrate added to the previous filtrate   Enough ammonium sulphate is added to the combined filtrates to bring the ammonium sulphate concentration up to 20 per cent by weight   The precipitated protein is then removed by filtration through a thin layer of celite on a Buchner funnel   All the virus protein is retained on the celite and can be removed by extracting three times with 0 1 m sodium phosphate solution at pH 7   The filtrate is adjusted to pH 4 5 by the addition of 3 m sulphuric acid and filtered through a thin layer of celite   The celite filter cake is then suspended in 300 cubic centimeters of water, the reaction being adjusted to pH 8 by the addition of an aqueous suspension of 5 per cent calcium oxide, and filtered with

suction through celite on a Buchner funnel   The celite filter cake is extracted with water at pH 8 and should yield a practically colorless opalescent solution   The protein is then crystallized by adding to 750 cubic centimeters of the solution 75 grams of solid ammonium sulphate, then 6 cubic centimeters of a solution of 5 per cent glacial acetic acid in 0 5 saturated ammonium sluphate, and finally 20 cubic centimeters of saturated ammonium sulphate solution

The procedure above may vary with the plants used   In the extraction of the tobacco-mosaic virus, plants inoculated when they are young and extracted about 4 weeks after inoculation give higher yields of pure crystals than plants inoculated when old   The pH of the solutions during extraction should be carefully controlled and should never be allowed to become greater than pH 8 5   In the more alkaline solutions the proteins are denatured with loss of infective power

Thornberry (1938) has described a modification of Stanley's method in which the previously frozen pulp is heated at 40°C before extraction

Vinson, McReynolds, and Ginguich (1939) recommend the use of solid sodium sulphate instead of ammonium sulphate for salting out the virus in crystalline form   They point out that the use of a nitrogenous salt to salt out a nitrogenous body is not desirable because of the danger of including some of the salting agent in the precipitate   They believe that the higher nitrogen content (20 per cent) reported for earlier isolations of the virus as compared with later estimates (16 7 per cent) can be explained on the basis of admixtures of ammonium sulphate which has a nitrogen content of 21 2 per cent

Solid sodium sulphate may be used for salting out the virus from fractions purified by any one of several methods   The initial precipitation from the expressed juices may be made with lead acetate (Vinson and Petre 1931), with safframin (Vinson 1932), with acid (Vinson 1936), or with solid anhydrous sodium sulphate following acidification to pH 4   The precipitate is then dispersed in a dilute solution of sodium phosphate at pH 7 After adjusting to pH 4, the virus is precipitated by adding the solid sodium sulphate

Most of the ash may be removed from the precipitate by washing with dilute acetic acid at pH 3 5, and the brown pigment is

readily removed by shaking a neutral phosphate dispersion of the crystalline virus with a volume of ether equal to about 30 per cent of the suspension and removing the ether by centrifuging

The chemical and physical properties of the viruses isolated by any of these methods may be studied, and the purified virus may be used in direct inoculation studies So far, the only viruses that have been obtained in crystalline form are readily transmitted by artificial sap inoculation Viruses that have been transmitted only by insects or by grafting may offer greater difficulties

The proof of the virus nature of those diseases which have been transmitted only by grafting obviously does not meet the requirements stated above These diseases are assumed to be caused by viruses merely on the basis of general similarity to other known virus diseases No satisfactory method of complying with Koch's postulates has been devised for this group of diseases If no insect vectors are ever found for these diseases, the isolation of the virus proteins and their use for reinoculation possibly may provide a means of proving their true nature

RULES OF PROOF FOR INSECT TRANSMISSION

Just as bacteria have been described without adequate proof, as being pathogenic, so have many species of insect been reported, with insufficient evidence, to be vectors of plant diseases Incomplete reports often remain unverified and lead to confusion in the literature It is desirable, therefore, that certain definite requirements be met before it is concluded that an insect is a vector of a plant pathogen It is believed that the following requirements constitute the minimum for adequate proof of insect transmission of a plant disease

1 A close, although not necessarily a constant, association of the insect with diseased plants must be demonstrated

2 It must be demonstrated that the insect also regularly visits healthy plants under conditions suitable for the transmission of the disease

3 The presence of the pathogen or virus in or on the insect in nature or following visitation to a diseased plant must be demonstrated

4 The disease must be produced experimentally by insect visitation under controlled conditions with adequate checks

When evidence is presented that an insect is a vector of a plant disease, it should always meet the above four requirements

It is equally necessary that the postulates of Koch be observed, for if there is an error in the diagnosis of the disease the remainder of the evidence is invalidated

SUPPLEMENTARY DATA

When an insect is incriminated as a vector of a plant disease, its relative importance in relation to other agents of transmission always should be determined in so far as possible, for only when this is known can the discovery be utilized effectively in a practical plan for controlling the disease   It is important also to determine whether the insect is a vector of primary inoculum or of secondary inoculum or of both   An insect that is a vector of primary inoculum may be of much greater significance in the epiphytology of a disease than one which is concerned only with the dissemination of secondary inoculum

In Chap III, it was shown that insects may influence the development of plant diseases in several ways   The insect may serve only as an agent of dissemination of the pathogen, or it may also be responsible for inoculation, for ingression, and for preservation of the pathogen over periods of unfavorable environment   The extent to which the insect performs each of these various functions should be determined

The ability of a suspected vector to transmit a disease should be tested in all stages of development   It has been shown that the ability of certain vectors to acquire the inoculum, or to transmit it, varies greatly with age   For example, *Thrips tabaci*, the vector of spotted wilt, cannot acquire the virus by feeding as an adult on infected plants but acquires it readily in the larval stage   Having acquired the virus as a larva, the insect remains infective through metamorphosis and transmits the virus as an imago   As another example may be mentioned the tingid bug (*Piesma quadrata*), the vector of sugar-beet leaf curl, which is unable to transmit the virus in the larval stage but readily acquires and transmits it as an adult   The reverse of this situation exists in the case of certain toxicogenic insects which are toxiniferous only in the nymphal stage   Thus it has been demonstrated that psyllid yellows of potatoes is caused only by the nymph of *Paratrioza cockerelli*, the adult psyllid being unable to cause the disease

It has been demonstrated by several workers that there are strains within a species of insect, some of which transmit a virus readily whereas others are totally unable to do so   The recognition of this fact makes it imperative that more than one strain of a species be tested, especially when negative or inconsistent results are obtained with a suspected vector

TAXONOMIC PROBLEMS

The importance of correct identification of the insects studied as possible vectors cannot be overemphasized   Much confusion has been caused by incomplete or incorrect identification of newly discovered vectors   Insect taxonomy is a matter for the specialist, and critical identification of species on which significant data are published should not be attempted by the novice   The best plan is to submit carefully chosen specimens to a well-recognized authority on the particular group of insects concerned   When the data are published, the authority responsible for the identification should be given   Smith (1937) has discussed the importance of this aspect of the problem and has emphasized the need for permanent reference collections of insect vectors of plant diseases   He states

To be certain of the specific identity of an insect vector is just as important in the problems of identification and means of dispersion of a given virus disease as in those problems presented by any other injurious insect   Whenever, in pathological experiments, the ability of an individual insect to transmit a particular virus has been demonstrated, the insect involved seems to possess a value to the virus problem approaching that of a type as designated by a taxonomist describing a new species, and representatives of such specimens should be preserved for future reference   This is especially important when there is any doubt as to the identity of the species represented, or when it belongs to a group in which related species might be confused

In the publication of the results of transmission tests an author could indicate the location of representatives of the experimental insects together with the accession number or other data by which the material may be located   The insects selected for preservation could be taken from any of the controlled experiments where positive results were obtained, particularly if from pure-line-bred stock   Whenever insects are submitted to the taxonomist for identification, ample material should be included, so that he will have no excuse for not returning

duplicates if the experimenter is interested in having them for reference or exchange

THE IMPORTANCE OF FIELD OBSERVATIONS

The methods used in investigating problems of insect transmission vary with the diseases and insects being studied   Some problems are well adapted to study in greenhouse and laboratory, while others must be investigated under field conditions   Whenever possible, greenhouse and laboratory studies should be supplemented by field experiments under conditions as nearly normal as can be obtained   In the investigation of any problem of insect transmission, extensive and thorough observations of the disease as it develops in nature and of the habits of the associated insects are of paramount importance   Casual observations at irregular intervals are not sufficient to give a complete picture of the disease and the phenomena associated with its transmission   The best results are obtained when one, so to speak, lives with the problem until he knows all its ramifications   Observations apparently insignificant at the time often prove to be keys to the solution of a difficult problem   This is true of almost any biological problem but applies particularly to investigations of this kind in which the worker is likely to be relatively unfamiliar with the behavior of either the disease or the associated insects

GREENHOUSES AND CAGES

Since virus diseases of plants are so universally transmitted by insects, the phenomena of insect transmission has assumed a very prominent place in their study   This has resulted in the development of a number of special techniques for the purpose   Most virus diseases are well adapted to greenhouse study, and much of the work on insect transmission is done in greenhouses

The two most important principles to be observed, in the study of insect transmission of virus diseases in greenhouses, are that an adequate supply of vigorous normally growing plants be available and that means be provided for adequate insect control   Normal vigorous plants are necessary because of the extreme importance of symptoms in the study of virus diseases   Unless the plants are vigorous and growing normally, symptoms lose much of their value as criteria in virus studies

The necessity for insect control is obvious but is sometimes disregarded. Reliable results cannot be obtained in greenhouses overrun with aphids, white flies, red spiders, thrips, or other arthropods. A regular routine of fumigation is necessary. In order to preserve cultures of insects for study, more than one house or compartment must be available. The standard nicotine fumigation for aphids and hydrocyanic acid gas for other insects are the usual methods.

The plan of construction most commonly used for greenhouses is not well adapted to the study of insect transmission. A greenhouse with several insect-proof compartments opening upon a central corridor is one of the most satisfactory arrangements.

Fig. 233 —Plan of a greenhouse of a type desirable for work with insect transmission of plant diseases. The separate compartments allow separation of diseased and healthy plants and different kinds of insect. It also allows for partial fumigation and other necessary operations. (*After Samuel, Bald, and Pittman*)

The plan of such a greenhouse designed for this kind of work is shown in Fig. 233. All ventilators should be provided with screens to prevent the entry of insects from the outside and the escape of experimental insects.

In studying insect transmission of a disease, it is obviously necessary to control all other possible means of transmission. For this reason, it may be necessary to use sterilized soil. Many different kinds of plant pathogen may survive in the soil and serve as unexpected sources of infection. Moreover, many insects that may serve as possible vectors may be found in non-sterilized soil.

Some of the viruses are highly infectious, but most of them require wounds for infection. The necessary wound in some cases may be the mere breaking of a trichome. Many fungi and bacteria also require wounds for infection. Therefore, it usually is important that experimental plants be handled with

extreme care to avoid accidental infection as a result of unnecessary wounding

The different types of cage used in rearing insects are so numerous that no attempt is made to describe them here   One beginning work in this field will do well to consult the manuals published by Peterson (1934, 1937)   Wire screen, cheesecloth, and glass are the most common materials used for making cages A cloth, originally used for shading tobacco and now used extensively in commercial aster growing, is good for this purpose Cellophane is proving a very satisfactory material in the construction of cages that are not too much exposed to the weather
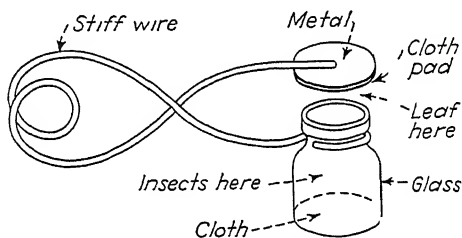
Fig 234 —A simple type of microcage designed for feeding a small number of insects on a localized area of a plant   The cage is illustrated in the sprung or open position   (*After Peterson*)

The variety of useful cages that can be made from this material supplemented with "Scotch tape," gauze, and other easily obtainable materials is limited only by the ingenuity and dexterity of the worker   Cellophane has the advantage of being relatively cheap, light, and very transparent   When plants are grown under cages, the reduced light intensity is often a limiting factor in normal growth   Peterson (1934) has compared the light transmission of various materials used in making insect cages   Cellophane had the greatest light-transmitting power of all the materials tested   When greater strength is desired, screen wire infiltrated with cellophane may be used, but the light transmission is reduced by nearly one-half

When it is desirable to feed insects upon localized regions of a plant, some kind of microcage is necessary   The form of the cage will be determined by the insects and plants to be used Convenient microcages have been described by F F Smith (1931), K M Smith (1932), Samuel, Bald, and Pittman (1930), Giddings (1939), and others   A satisfactory type of microcage

is illustrated in Fig 234 The cage designed and used by Giddings (1939) for feeding leaf hoppers on individual sugar beet leaves is shown in Fig 235

For the collection of small insects and for transferring them from cage to cage, a suction collector of the type illustrated in Fig 236 is indispensable Several modifications of this device have been described, but the type illustrated appears to be the most satisfactory for general use
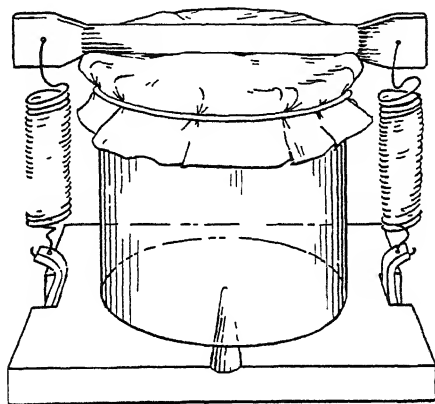
Fig 235 —A microcage designed and used for feeding a small number of leaf hoppers on individual sugar-beet leaves The cage is composed of a small glass cylinder closed with gauze at one end and held firmly against a small piece of glass by two springs and specially made metal clamps The edges of the glass are ground to prevent bruising or cutting, and the glass plate is grooved to take the leaf mid-rib or petiole (*After Giddings*)

INSECT TRAPS

In the study of insects in relation to the development of diseases, it is often desirable to obtain data on their abundance and movement under normal field conditions Some insects winter in definite restricted localities and spread gradually into new areas as the growing season advances, whereas others appear suddenly as a result of migration Still others are dispersed by wind currents The abundance of a given insect vector at a given time and its method of dispersal are obviously significant in the epiphytology of the disease Insect traps of various kinds are used for obtaining such data

One of the most useful types of insect trap for determining the prevalence of insects is the light trap In this trap, the insects

are caught at night, being attracted by a light and entrapped in a cyanide jar   Many different designs of varying degrees of
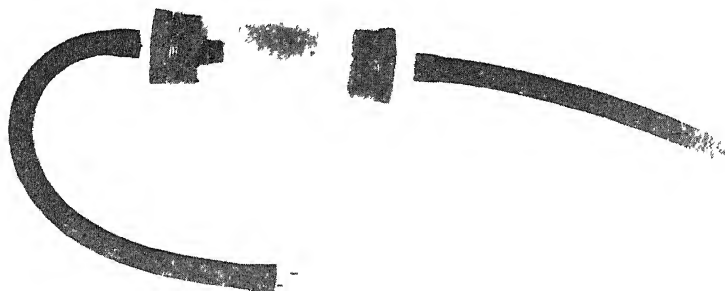
FIG 236 —A simple and practical insect collector of the suction type that is indispensable for handling individual insects of the kind usually serving as vectors of plant diseases   Its structure and operation are self-evident from the picture

complexity have been used   A simple, but satisfactory light trap for general use is illustrated in Fig 237   Other designs to
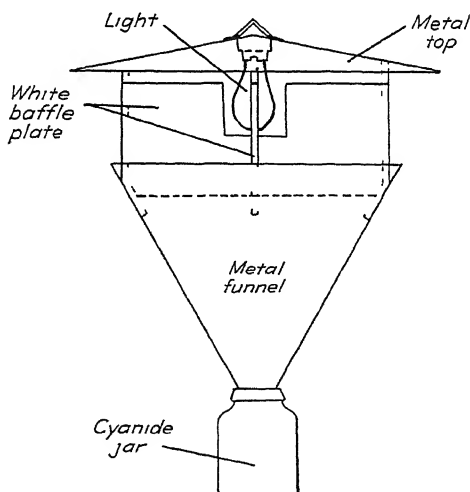
FIG 237 —A diagram showing the structure of a simple but satisfactory light trap   (*After Peterson*)

meet special demands are described by Peterson (1934)   The cyanide jar is prepared by placing potassium or sodium cyanide,

about ¼ inch deep, in the bottom of the jar and then adding a thin layer of moist plaster of Paris, which soon hardens   Enough hydrocyanic acid gas will diffuse through the plaster of Paris to kill the entrapped insects   When in use, the jar should contain a quantity of loosely crumpled strips of blotting paper, which will increase the efficiency of the cyanide and prevent injury to the trapped insects

A trap for the study of the movement of insects by wind currents has been designed by Fulton and Chamberlin (1931)
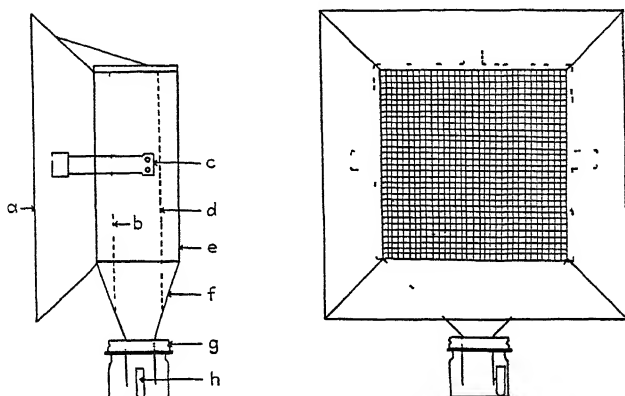
FIG 238 —A sketch showing the structure of the wind trap of Fulton and Chamberlin   *a*, baffle plate, *b*, hardware cloth ⅛ inch mesh, *c*, angle brace *d*, wire screen, 16 mesh, *e*, wire screen, 22 mesh, *f*, funnel, *g*, screw cap for mason jar, *h*, cyanide bag   (*After Fulton and Chamberlin*)

In this trap, the insects are blown by the wind through a series of wire screens in which they become entangled, finally falling into a cyanide jar   The trap is installed so that it rotates with the wind, the front of the trap being held facing the wind by a "weather-vane" attachment.   The plan of construction is shown in Fig 238   The trapping of insects larger or smaller than those desired may be avoided to some extent by the proper arrangement of screens of the appropriate size mesh

MICROBIOLOGICAL METHODS

The nature of insect transmission, *i e* , whether mechanical or biological, should be definitely established   If the transmission is biological, the physiological, anatomical, and histological relationships between pathogen and vector should be determined   This will probably involve a study requiring several

different kinds of technique   It will require a study in which
the pathogen is cultured from various parts of the insect's body
Insect vectors are usually contaminated with numerous micro-
organisms other than the pathogenic one   Many of these will
grow on artificial media more rapidly than the pathogen, a fact
making it difficult to isolate the pathogen in pure culture or to
demonstrate its presence   Differential or selective media are
very useful and often necessary if this phase of the investigation
is to be successful

Differential or selective media are those which favor the growth
of the organism desired and inhibit the growth of the undesired
contaminants   Many different kinds of selective media have
been used   One of the simplest of these is made by modifying
the acidity reaction   Fungi often may be freed from bacterial
contamination by the use of a medium with acidity near or
slightly below pH 4 0   This method is based on the fact that
most bacteria will not grow well on acid media whereas most
fungi are not appreciably inhibited   A 25 per cent solution of
lactic acid is commonly used for acidifying the medium

Fungi and Gram-positive bacteria may be inhibited by adding
to the medium a triphenylmethane dye such as crystal violet
Concentrations somewhere between 1 to 50,000 and 1 to 200,000
are usually sufficient to inhibit the Gram-positive species without
greatly inhibiting the Gram-negative ones   This medium is
particularly helpful in isolating pathogenic bacteria from mixtures
of saprophytic ones, for the majority of pathogenic bacteria are
Gram-negative whereas the more rapidly growing contaminating
bacteria are usually Gram-positive

It may be necessary to devise a special selective medium to
meet the requirements of the particular problem   This can be
done only by experimentation   Much time can be saved, how-
ever, by utilizing the experience of others, making whatever modi-
fications in known formulae the particular situation demands
In devising a selective medium, the physiological characters of
the organism to be cultured and those to be inhibited should be
studied with particular reference to tolerance for such things
as acidity, bacteriostatic dyes, host extracts, high concentrations
of salts, or other special ingredients

Two examples of selective media helpful in isolating certain
bacterial plant pathogens are given here   For additional

formulae of media suitable for specific purposes, see Levine and Schoenlein (1930), Rawlins (1933), Riker and Riker (1936), and the Committee on Bacteriological Technique, Society of American Bacteriologists (1938)

Patel's Agar (Patel 1926) —A selective medium useful in isolating *Phytomonas tumefaciens* and several other bacterial plant pathogens from the soil and other contaminated material

Distilled water	1,000 cc
Agar	15 g
Sodium taurocholate	3 g
Peptone	10 g
Dextrose	20 g
1 to 1,000 aqueous solution of crystal violet	2 cc

Melt the agar in the water by autoclaving, add the other ingredients, adjust to pH 7, filter, and tube and sterilize in the autoclave

Ivanoff's Agar (Ivanoff 1933) —A synthetic medium useful in isolating *Phytomonas stewarti* from soil and other contaminated material

Distilled water	1,000 cc
Agar	17 0 g
Glycerol	30 0 cc
Ferric ammonium citrate	10 0 g
Sodium taurocholate	3 0 g
Sodium chloride	15 0 g
Sodium sulphate	2 5 g
Potassium dibasic phosphate	2 5 g
Calcium chloride	1 0 g
Magnesium sulphate	0 1 g

Add the ingredients to the agar melted in the water, filter, and tube and sterilize in the autoclave

Pathogenic organisms may be isolated from old and badly contaminated plant or insect material by using the selective action of the host plant   In this method, the host plant is inoculated with the mixed culture taken directly from the contaminated material, if conditions are suitable, infection will occur, forming a fresh lesion from which the pathogen may be isolated by the usual methods of tissue cultures or dilution plates   If the newly formed lesions are of a nature that permits rapid growth of contaminating organisms, it may be necessary to

repeat the process with successive isolations until the selective action of the host has permitted the pathogen to outgrow the contaminating organisms This method has been used with success by Fulton (1920) in isolating *Phytomonas citri* (Hasse) Bergey *et al* from the soil and by Leach (1930) in isolating *Erwinia carotovora* from the soil and from the various developmental stages of seed-corn maggot

In the study of the relationships between pathogen and vector, it may be necessary to dissect out particular organs of the insect This requires considerable skill and dexterity depending upon the size and nature of the insect Dissections are usually made under the binocular microscope with the insect secured to a block of wax Pins may be used in securing the specimen, or it may be partly embedded in the melted wax which is later cooled If the dissection is made with the view of obtaining cultures of the associated microorganism, it may be desirable to surface-sterilize the insect by immersing it successively in 95 per cent alcohol, a mercuric chloride solution (1 to 1,000) and again in 95 per cent alcohol The internal organs of insects may dry very rapidly when exposed to dry air and usually become difficult to handle This trouble may be avoided by covering the specimen with a sterile saline solution

When pathogens or other microorganisms live symbiotically with their vectors, it is of interest to know whether or not they are transmitted within the egg The chorions of most insect eggs are relatively impervious to aqueous solutions, and eggs may be surface-sterilized by immersing them in a solution of mercuric chloride (1 to 1,000) The mercuric chloride solution is then removed by washing the eggs in sterile distilled water The time required for surface sterilization without injury must be determined for each kind of egg The eggs of the seed-corn maggot and cabbage maggot may be immersed in this solution for at least 2 hours without injury (Leach 1926) This is much longer than is necessary for effective surface sterilization

HISTOLOGICAL METHODS

Microbiological studies in which the microorganisms are isolated from the insect must be supplemented by histological studies, if the more detailed anatomical relationship between pathogen and vector is to be learned This usually is accom-

plished best by cutting serial sections from material embedded in paraffin and staining them with a differential stain Simple smears may be made and stained on glass slides by dissecting out the various organs concerned This is useful as a rapid method of determining the presence of the microorganism but is not so satisfactory as the paraffin method for more critical studies Similar histological studies of plant tissue also are frequently necessary in the study of insect transmission of plant diseases In a study of the mechanism of feeding by insect vectors, both insect and plant tissues must be studied The techniques for the study of insect and plant histology are too numerous for an extensive treatment in this book The student should consult the more comprehensive guides to histological technique Some of the most helpful guides are those published by the following authors Chamberlain (1932), McClung (1929), Kingsbury and Johannsen (1927), Mallory and Wright (1924), Kennedy (1932), and Becker and Roudabush (1935)

Success will depend to some extent upon the choice of killing fluids and staining formulae There are numerous formulae from which to choose, and the choice will depend largely upon the material being studied and the worker's preference The following formulae have proved satisfactory when used by the author for the material indicated

Fixing Solutions —The Nawaschin solution is one of the most satisfactory killing and fixing solutions for plant tissues The solution must be freshly prepared for each lot of material Fix for 24 hours, and wash in running water for 24 hours

Nawaschin Solution

1 % chromic acid solution	10 0 cc
16 % formalin solution	4 0 cc
Glacial acetic acid	1 0 cc

If material must be killed and fixed in the field at the time of collection, the formaldehyde-acetic acid-alcohol solution is satisfactory No washing in water is necessary, and the material may be kept for some time in the fixing solution without injury

Formalin-Acetic Acid-Alcohol Solution

Formalin	10 0 cc
Glacial acetic acid	5 0 cc
Alcohol 50 %	200 0 cc

Zenker's fixing solution is one of the most satisfactory fixing fluids for insect material

Zenker's Solution

Solution I

Potassium dichromate	2 5 g
Sodium sulphate	1 0 g
Mercuric chloride	5 0 g
Distilled water	100 0 cc

Solution II

Glacial acetic acid	5 0 cc

Mix solution I and II just before using   Fix in the solution for 12 to 48 hours, and wash in running water for 12 to 48 hours Place in 50 per cent alcohol for 3 hours and 70 per cent alcohol for 3 to 24 hours, keeping the material in the dark while in the alcohol solutions   Transfer to 70 per cent alcohol, and add a saturated solution of iodine in 10 per cent alcohol, drop by drop, until the iodine solution is no longer decolorized   The solution may be poured off and replaced with fresh 70 per cent alcohol several times during this process   When iodine treatment is complete, transfer to 80 per cent alcohol and complete the dehydration process

When it is not convenient to use Zenker's solution or when the insects must be left for a long time in the killing fluid, the formalin-acetic acid-alcohol solution may be used   A slightly modified formula known as Dietrich's solution has been used for several different kinds of insect with excellent results

Dietrich's Solution

Alcohol 95 %	30 0 cc
Glacial acetic acid	2 0 cc
Formalin	10 0 cc
Distilled water	60 0 cc

In a study of the mechanics of feeding of insect vectors such as aphids, it is necessary to kill and fix the specimens so that the stylets are not withdrawn from the tissues   A satisfactory method has been described by Dykstra and Whitaker (1938) Leaves and stems on which the insects are feeding are cut from the plant with as little disturbance of the insects as possible

The entire specimen is dipped in chloroform, removed immediately, and immersed in formalin-acetic-alcohol for 24 hours The specimens are deaered with an exhaust pump in this solution then washed in dioxane over calcium chloride for 24 hours After dehydration, the material is cleared in the following series of dioxane and xylol, leaving it 10 to 15 minutes in each mixture

    1 Xylol 1 part, dioxane 4 parts
    2 Xylol 2 parts, dioxane 3 parts
    3 Xylol 3 parts, dioxane 2 parts
    4 Xylol 4 parts, dioxane 1 part

The material is then removed to pure xylol and embedded in paraffin in the usual manner

The use of dioxane for dehydration is based on the schedule described earlier by McClung (1936) and by McWhorter and Weier (1936)   The substitution of dioxane for alcohol prevents the tissues from becoming brittle, so that ribbon sections can be cut of heavily lignified tissues without disturbing the delicate mouth parts of the insects embedded in the tissue   The method as applied in the above study has been described also by Whitaker (1937)   A more complete discussion of the dioxane technique has been published by Mossman (1937), who was largely responsible for introducing the method to American workers

Staining.—Many different staining formulae are used for demonstrating the presence of bacteria or fungi in plant tissue One of the more satisfactory of several used by the author is the carbol-fuschin and light-green combination   With this stain, bacteria or fungi are stained a deep red, and cellulose cell walls are stained a bright green   The striking contrast of these colors is of great advantage in locating the microorganisms if they are present in small numbers and allows very sharp differentiation between the pathogen and the tissues of the host plant

Carbol Fuschin and Light Green

Fuchsin	1 0 g
Alcohol 95 %	10 0 cc
Carbolic acid crystals	5 0 g
Distilled water	100 0 cc

Stain sections, removed from 10 per cent alcohol, for 3 minutes Rinse in water, and dehydrate by passing rapidly through alcohol series, being careful not to destain too much   From absolute

alcohol, transfer to a saturated solution of light green in clove oil
Clear by rinsing with clove oil and mount in balsam

A carbol-fuchsin and picric acid formula recommended by
Hertig and Wolbach (1924) has proved satisfactory for demon-
strating the presence of bacteria in the body of Dipterous insects
(Leach 1931, 1933)

Carbol Fuchsin and Picric Acid

Solution I

Basic fuchsin	0 5 g
Carbolic acid crystals	1 0 g
Aniline oil	0 5 cc
Alcohol 30 %	100 0 cc

Dissolve fuchsin in alcohol, and add remaining reagents

Solution II

Picric acid	Saturated aqueous solution

Sections should be steamed over boiling water for 5 minutes
in a few drops of solution I poured on the slide   Wash off excess
stain in tap water   Decolorize and differentiate by pouring
formalin over the sections, a few drops at a time, until the excess
color is removed   Rinse in water and counterstain for 1 minute
in solution II   Dehydrate quickly in 95 per cent alcohol, abso-
lute alcohol, and xylol   Mount in balsam

The Gram-Weigert stain (Mallory and Wright 1924) has given
excellent results in demonstrating the presence of yeasts, fungus
spores, and Gram-positive bacteria in bark beetles and other
Coleoptera   It also gives excellent differentiation of the insect
tissues   It is not satisfactory if the microorganisms concerned
are Gram-negative

Gram-Weigert Stain (Modified)

Solution I

ALUM HAEMATOXYLIN

Haematoxylin	1 0 g
Ammonia alum (sat aq sol)	100 0 cc
Water	300 0 cc
Potassium permanganate (0 25 % aq sol)	10 0 cc
A small thymol crystal	

Pulverize haemotoxylin, and dissolve it with the ammonia alum in the water with aid of heat   Cool and add potassium permanganate and then the thymol crystal   The stain is ready for use at once   As the stain ripens, it may be necessary to add a little of the saturated alum solution   Filter each day before using

Solution II

    Eosin   5 % aqueous solution

Filter each day before using

Solution III

<div align="center">ANILINE METHYL VIOLET</div>

Solution A		Solution B
Absolute alcohol	33 0 cc	Saturated aqueous solu-
Aniline oil	9 0 cc	tion of methyl violet
Methyl violet	In excess	

Mix 1 part of solution A and 9 parts of solution B not longer than 2 weeks before using   Filter each day before using

Solution IV

<div align="center">LUGOL S SOLUTION</div>

Iodine	1 0 g
Potassium iodide	2 0 g
Distilled water	100 0 cc

Stain sections for 3 minutes in alum-haematoxylin solution Rinse in running water   Stain 3 minutes in 5 per cent eosin solution   Rinse off surplus stain in running water   Stain in solution III (aniline methyl violet) for 5 minutes   Wash 1 minute in running water   Immerse in Lugol's solution for 1 minute   Rinse in running water   Drain off excess water, dry back of slide, and clear in a solution of 1 part xylol and 1 part aniline oil   Agitate slides until excess methyl violet stain is removed   Wash thoroughly in xylol to remove every trace of aniline oil, and mount in balsam

MISCELLANEOUS TECHNIQUES FOR SPECIAL PURPOSES

Radioactive Substances —Hamilton (1935) has introduced a novel technique for the study of the course of ingested food in the insect's body in relation to virus transmission   This involves

feeding the insect vectors on a medium containing polonium, a radioactive substance the presence of which can be detected with a fluoroscope   This substance was ingested from agar by *Myzus persicae* and transmitted to the plants on which it subsequently fed in quantities that excluded the possibility of simple mechanical transmission   Recent developments in methods for producing radioactive forms of many of the common elements should provide materials suitable for the more extensive use of this technique in the study of the physiology of insects in relation to virus transmission

Differential Killing —When microorganisms survive in the body of an insect through metamorphosis, they are usually reduced to relatively small numbers during certain stages   The microbes do not die, but their growth and multiplication is inhibited by the life processes of the insect   When in this condition they may be difficult to locate by cultural or histological methods   Aid in tracing the microorganisms may be gained by subjecting the insect at the critical stage to subfreezing temperature   The low temperature will usually kill the insect but will not injure the microorganism   If the specimen is then returned to a more moderate temperature, the microorganism, unless it is an obligate parasite, being no longer inhibited by the living tissues of the insect, will begin to grow and can be more easily detected   This method was used successfully by the author (Leach 1933) in tracing the survival of bacteria in the puparia of the seed-corn maggot

In the study of symbiotic relationships between insects and microorganisms it is often desirable to obtain insects free of their symbiotes   This may present many difficulties   Cleveland in his investigation of the symbiotic relationships between termites and protozoa devised a number of differential treatments by means of which termites were freed of their intestinal protozoa   One method consisted in incubating the termites at 36 degrees centigrade for 24 hours, a treatment that killed the protozoa without injuring the termites   Prolonged starvation of the termites also was often successful   The most satisfactory method, however, consisted in placing the insects in an atmosphere of almost pure oxygen under pressure of 3 or 4 atmospheres for 1 or 2 hours   To what extent these methods can be used with other insects and other microorganisms remains to be determined

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APPENDIX

In the following appendix, certain facts, pertinent to the subject of insect transmission of plant diseases, have been tabulated for convenient reference In Table I, the more important insect-transmitted plant diseases have been grouped in one column according to the causal agent, with numerical reference to their respective vectors listed in the opposite column In Table II, the vectors are grouped in one column, according to order and family, with numerical reference to the diseases transmitted, the latter being given in the opposite column In Tables III to V, certain representative insect-transmitted plant diseases are compared with respect to significant transmission phenomena In Table VI, a few representative animal diseases are compared in a similar manner A study of these tables should aid in giving a better perspective of the subject matter treated in detail in the text

TABLE I —SOME OF THE MORE IMPORTANT INSECT-TRANSMITTED PLANT
DISEASES AND THEIR RESPECTIVE INSECT VECTORS

Diseases	Vectors
Diseases caused by toxicogenic insects	**HEMIPTERA**
Anasa wilt of cucurbits (1)*	1 *Anasa tristis* De G
Froghopper blight of sugar cane (5)	**HOMOPTERA**
Green spotting of pineapple (2)	2 *Pseudococcus brevipes* Ckl
Hopper burn of potato and other plants (3)	3 *Empoasca fabae* Harris
Mealy-bug wilt of pineapple (2)	4 *Paratrioza cockerelli* Sulc
Psyllid yellows of potato (4)	5 *Thomaspis saccharina* Dist
Virus diseases	**ORTHOPTERA**
A virus disease of rape and ruta-baga (6)	1 *Melanoplus spp*
Abacá bunchy top (Musa virus 2) (57)	**THYSANOPTERA**
Abacá mosaic (18)	2 *Franklinella lycopersici* Andr
Alfalfa mosaic (Medicago viruses 1 and 2) (50)	3 *Franklinella moultoni* Hood
Aster yellows (Callistephus viruses 1 and 14) (36, 64, 65)	4 *Franklinella occidentalis* Perg
	5 *Thrips tabaci* Lind
	HEMIPTERA
	6 *Lygus pratensis* L
	7 *Piesma cinerea* Say

* The numbers in parentheses following the name of the disease refer to the numbers of the insect vectors in the opposite column

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TABLE I —SOME OF THE MORE IMPORTANT INSECT-TRANSMITTED PLANT
DISEASES AND THEIR RESPECTIVE INSECT VECTORS —*(Continued)*

Diseases

Virus diseases (continued)

Aucuba mosaic of potato (Sola-
num virus 9) (54)

Banana bunchy top (Musa virus
1) (57)

Banana mosaic (Musa virus 3)
(57)

Bean mosaic (Phaseolus virus 1)
(18, 22, 27, 28, 32, 44, 47, 48,
50, 54, 64)

Bean yellow mosaic (Phaseolus
virus 2) (48, 50)

Beet mosaic (Beta virus 2) (27,
38)

Blackberry dwarf (Rubus virus
5) (34)

Cabbage ring spot (Brassica virus
1) (54)

Cassava mosaic (Manihot virus
1) (29, 30)

Cauliflower mosaic (Brassica virus
3) (15, 18, 19, 23, 32, 35, 53,
54, 61, 63)

Celery calico (Apium virus 2) (18)

Common mosaic of pea (Pisum
viruses 2 and 2C) (27, 48, 50,
54)

Corn mosaic (Zea virus 1) (58)

Cranberry false blossom (Vaccin-
ium virus 1) (42)

Cucumber mosaic (Cucumis virus
1) (18, 48, 53, 54, 55, 67, 69)

Curly top of sugar beet (Beta
virus 1) (43)

Dahlia mosaic (Dahlia virus 1)
(54)

Enation mosaic of pea (Pisum
virus 1) (50)

Fiji disease of sugar cane (Sa-
charum virus 2) (59, 60)

Freesia mosaic (Freesia virus 1)
(16)

Grape mosaic (Vitis virus 1) (46)

Vectors

8 *Piesma quadrata* Fieb

HOMOPTERA

9 *Aceratagallia   sanguinolenta*
(Provancher)

10 *Amphorophora rubicola* (Oest-
lund)

11 *Amphorophora rubi* Kalt

12 *Amphorophora   sensoriata*
Mason

13 *Anuraphis   padi* L   (*Aphis
pruni*)

14 *Anuraphis tulipae* B de Fonsc

15 *Aphis apigraveolens* Theob

16 *Aphis convolvul* Kalt

17 *Aphis forbesi* Weed

18 *Aphis gossypii* Glov

19 *Aphis graveolens* Essig

20 *Aphis laburni* Kalt   (*Aphis
leguminosae* Theo)

21 *Aphis mardis* Fitch

22 *Aphis medicaginis* Koch

23 *Aphis middletonii* Thomas

24 *Aphis pomi* De G

25 *Aphis rhamni* Boyer (*abbre-
viata* Patch)

26 *Aphis rubicola* Oestl (*rubi-
phila* Patch)

27 *Aphis rumicis* L

28 *Aphis spiraccola* Patch

29 *Bemisia   gossypiperda   var
mosaicivectura* Ghesq

30 *Bemisia nigeriensis* Corb

31 *Bemisia gossypiperda* Misra
and Lamba

32 *Brevicoryne brassicae* L

33 *Capitophorus fragaefolii* Ckl

34 *Capitophorus   tetrarhodus*
(Walker)

35 *Cavariella capreae* Fabr

36 *Macrosteles divisa* (Uhl)

37 *Cicadulina mbila* Naude

38 *Cicadulina storeyi* China

39 *Cicadulina zeae* China

TABLE I —SOME OF THE MORE IMPORTANT INSECT-TRANSMITTED PLANT
DISEASES AND THEIR RESPECTIVE INSECT VECTORS —(*Continued*)

Diseases | Vectors

Virus Diseases (continued)

Henbane mosaic (Hyoscyamus virus 1) (54)

Iris mosaic (Iris virus 1) (48, 54)

Leaf curl of cotton (Gossypium virus 1) (31)

Leaf curl of sugar beet (Beta virus 3) (8)

Leaf curl of tobacco (Nicotiana virus 10) (31)

Lettuce mosaic (Lactuca virus 1) (51, 54)

Little peach (Prunus virus 1*A*) (52)

Mosaic of crucifers (Brassica virus 4) (32, 54)

Mottle of corn (Zea virus 3) (37, 38, 39)

Peach mosaic (Prunus virus 5) (13)

Peach yellows (Prunus virus 1) (52)

Peanut rosette (Arachis virus 1) (20)

Pelargonium leaf curl (Pelargonium virus 1) (49)

Pineapple yellow spot (Ananas virus 1) (5)

Potato leaf roll (Solanum virus 14) (27, 53, 54, 55)

Potato mosaic (Solanum virus 3) (25)

Potato spindle tuber (Solanum virus 12) (1, 6, 48, 54, 69, 70, 71, 72)

Potato streak (leaf drop) (Solanum viruses 2 and 3) (54)

Potato tuber blotch (Solanum virus 8) (54)

Potato unmottled curly dwarf (1, 6, 41, 48, 54, 69, 70, 71, 72)

Potato yellow dwarf (Solanum virus 16) (9, 48, 54)

Rape Savoy (6)

Raspberry leaf curl (Rubus viruses 3 and 3*A*) (26)

40 *Delphacodes striatella* Fall (*Libunia striatella* Fall)

41 *Euscelis exitiosus* (Uhler)

42 *Euscelis striatulus* Fall

43 *Eutettix tenellus* Baker

44 *Hyalopterus atriplicis* (L)

45 *Hysteroneura setariae* Thomas

46 *Lecanium corni* Bouche

47 *Macrosiphum ambrosiae* (Thomas)

48 *Macrosiphum gei* Koch (*solanifolii*) Ashm

49 *Macrosiphum pelargonii* Kalt

50 *Macrosiphum* (*Illinoia*) *pisi* Kalt

51 *Macrosiphum sonchi* L

52 *Macropsis trimaculata* Fitch

53 *Myzus circumflexus* Buckt

54 *Myzus persicae* Sulz

55 *Myzus pseudosolani* Theob

56 *Nephotettix apicalis* var *cincticeps* Motsch

57 *Pentalonia nigronervosa* Coq

58 *Peregrinus maidis* Ashm

59 *Perkinsiella saccharicida* Kirk

60 *Perkinsiella vastatrix* Breddin

61 *Rhopalosiphum melliferum* Hottes

62 *Rhopalosiphum prunifoliae* Fitch

63 *Rhopalosiphum pseudobrassicae* Davis

64 *Thamnotettix geminatus* Van D

65 *Thamnotettix montanus* Van D

66 *Deltocephalus dorsalis* Motsch

COLEOPTERA

67 *Diabrotica duodecimpunctata* Oliv

68 *Diabrotica vittata* Fabr

69 *Disonycha triangularis* (Say)

70 *Epitrix cucumeris* Harris

71 *Leptinotarsa decimlineata* Say

72 *Systena taeniata* (Say)

TABLE I —SOME OF THE MORE IMPORTANT INSECT-TRANSMITTED PLANT
DISEASES AND THEIR RESPECTIVE INSECT VECTORS —*(Continued)*

Diseases	Vectors
Virus diseases (continued)	
Raspberry yellow mosaic (Rubus virus 2) (10, 11, 12)	*(See preceding pages)*
Red raspberry mosaic (Rubus virus 1) (10, 11, 12)	
Rice dwarf (Oryza virus 1) (56, 66)	
Savoy of sugar beet (Beta virus 5) (7)	
Spotted wilt (Lycopersicum virus 3) (2, 3, 4, 5)	
Stock mosaic (Matthiola virus 1) (32, 54, 63)	
Strawberry crinkle (Fragaria virus 2) (33)	
Strawberry dwarf (Fragaria virus 4) (17)	
Strawberry witches'-broom (Fragaria virus 3) (33)	
Strawberry xanthosis (Fragaria virus 1) (33)	
Streak of corn (Zea virus 2) (37, 38, 39)	
Stripe of rice (Oryza virus 2) (40)	
Sugar-beet mosaic (Beta virus 2) (54, 27)	
Sugar-beet yellows (Beta virus 4) (27, 54)	
Sugar-cane mosaic (Saccharum virus 1) (21, 45)	
Tobacco mosaic (Nicotiana virus 1) (48, 53, 55)	
Tulip mosaic (Tulipa virus 1) (14, 48, 49, 54)	
Turnip mosaic (Brassica virus 2) (32)	
White-clover mosaic (Trifolium virus 1) (27, 50)	
Yellow dwarf of onion (Allium virus 1) (11, 18, 21, 24, 27, 32, 44, 45, 48, 50, 54, 62, 63)	
Yellow flat of lily (Lilium virus 1) (18)	

TABLE I —SOME OF THE MORE IMPORTANT INSECT-TRANSMITTED PLANT DISEASES AND THEIR RESPECTIVE INSECT VECTORS —(*Continued*)

Diseases

Bacterial diseases

Bacterial disease of willows (*Pseudomonas saliciperda*) (25)

Bacterial gall of Douglas fir (*Bacterium pseudosugae*) (9)

Bacterial rot of apples (*Phytomonas melophthora*) (37)

Bacterial wilt of corn (Stewart's disease) (*Phytomonas stewarti*) (13, 14, 15, 16, 17)

Bacterial wilt of cucurbits (*Erwinia tracheiphila*) (16, 19)

Bacterial wilt of Solanaceae (*Erwinia solanacearum*) (20)

Bacteriosis of the prickly-pear plant (*Erwinia cacticida*) (28, 29, 30, 31, 32)

Bean bacteriosis (*Phytomonas medicaginis* var *phaseolicola*) (1)

Black rot of crucifers (*Phytomonas campestris*) (34)

Fire blight (*Erwinia amylovora*) (2, 3, 4, 5, 6, 7, 8, 10, 11, 12, 18, 21, 22, 23, 24, 26, 27, 33, 35, 38, 41, 44, 46, 47, 48, 49, 50, 51, 52, 53, 54, 55, 56)

Olive knot (*Erwinia savastonoi*) (36)

Potato blackleg (*Erwinia carotovora*) (43, 45)

Soft rot of crucifers (*Erwinia carotovora*) (42)

The heart rot of celery (*Erwinia carotovora*) (39, 40)

Vectors

THYSANOPTERA

1 *Heliothrips femoralis* Reut

HEMIPTERA

2 *Adelphocoris rapidus* (Say)

3 *Campylomma verbasci* (Meyer)

4 *Lygus pratensis* L

5 *Orthotylus flavosparsus* (Sahlb)

6 *Plagiognathus politus* Uhl

7 *Poecilocytus basalis* Reut

HOMOPTERA

8 *Empoasca mali* Le Baron

9 *Chermes cooleyi* Gill

10 *Aphis avenae* Fay

11 *Aphis pomi* De Geer

COLEOPTERA

12 *Hippodamia convergens* Guer.

13 *Phyllophaga sp*

14 *Chaetocnema denticulata* Ill

15 *Chaetocnema pulicaria* Melsh

16 *Diabrotica duodecimpunctata* Oliv

17 *Diabrotica longicornis* Say

18 *Diabrotica soror* Le C

19 *Diabrotica vittata* Fabr

20 *Leptinotarsa decimlineata* Say

21 *Orsodacne atra* (Ahr)

22 *Attagenus piceus* Oliv

23 *Anthrenus sp*

24 *Glischrochielus fasciatus* Oliv

25 *Cryptorrhynchus lapathi* L

26 *Melanotus oregonensis* (Le C)

27 *Scolytus rugulosus* Ratz

LEPIDOPTERA

28 *Mimorista flavidissimalis* Grote

29 *Cactoblastis bucyrus* Dyar

30 *Cactoblastis cactorum* Berg

31 *Melitara prodenialis* Walker

32 *Melitara junctelinsella* Hulst

33 *Carpocapsa pomonella* L

34 *Plusia brassicae* Riley

DIPTERA

35 *Bibio albipennis* Say

TABLE I —SOME OF THE MORE IMPORTANT INSECT-TRANSMITTED PLANT DISEASES AND THEIR RESPECTIVE INSECT VECTORS —(*Continued*)

Diseases	Vectors
	36 *Dacus olea* Rossi
	37 *Rhagoletis pomonella* Walsh
	38 *Drosophila funebris* Fabr
	39 *Elachiptera costata* Leow
	40 *Scaptomyza grammum* Fall
	41 *Hylemyia antiqua* Meig
	42 *Hylemyia brassicae* Bouche
	43 *Hylemyia cilicrura* Rond
	44 *Hylemyia lipsia* Walker
	45 *Hylemyia trichodactyla* Rond
	46 *Pegomyia calyptrata* Zett
	47 *Cynomyia cadaverina* Desv
	48 *Musca domestica* L
	49 *Muscina assimilis* Fall
	50 *Muscina stabulans* Fall
	HYMENOPTERA
	51 *Formica fusca* L var *subsericea* Say
	52 *Formica pallidefulva* Latr subsp *schaufussi* Mayr var *incerta* Emery
	53 *Lasius niger* (L) var *americanus* Emery
	54 *Prenolepis imparis* Say
	55 *Polistes* sp
	56 *Vespula* sp
Fungus diseases	ORTHOPTERA
Blackleg of cabbage (*Phoma lingam*) (46)	1 *Oecanthus angustipennis* Fitch
Blue stain of coniferous trees (*Ceratostomella spp*) (34, 35, 36, 36a, 36b, 36c)	2 *Oecanthus niveus* De G
	3 *Chortophaga viridifasciata* var *australior* De G
	4 *Dissosteira carolina* L
Blue stain of spruce (*Ceratostomella piceaperda*) (34a)	5 *Encoptolophus texensis* Brun
	6 *Melanoplus differentialis* Thomas
Blue stain of Douglas fir (*Ceratostomella pseudotsugae*) (34b)	7 *Melanoplus femur-rubrum* De G
Brown stain of white fir (*Trichosporium symbioticum*) (42b)	8 *Melanoplus mexicanus* Sauss
	9 *Schistocerca americana* Drury
Brown stain of white fir (*Spicaria anomala* (42c)	10 *Schistocerca obscura* Fabr
	11 *Spharagemon cristatum* Scudd
Canker of apple (*Diplodia griffoni*) (26)	12 *Tomonotus aztecus* Sauss
	13 *Trimerotropis citrina* Scudd

TABLE I —SOME OF THE MORE IMPORTANT INSECT-TRANSMITTED PLANT DISEASES AND THEIR RESPECTIVE INSECT VECTORS —(*Continued*)

Diseases | Vectors

Fungus diseases (continued)

Chestnut blight (*Endothia parasitica*) (32, 33)

Cotton wilt (*Fusarium vasinfectum* Atk) (3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13)

Downy mildew of lima beans (*Phytophthora phaseoli* Thaxter) (48)

Endosepsis of figs (*Fusarium monilforme* var *fici*) (47)

Ergot of cereals and grasses (*Claviceps paspali*) (31, 44)

European canker (*Nectria galligena*) (26)

Inspissosis of citrus fruits (*Nematospora coryli*) (21, 24)

Perennial canker of apple (*Glocosporium perennans*) (26)

Smut of figs (*Aspergillus niger*) (30, 45)

Sooty mold of orange (*Capnodium citri* and other fungi) (25, 27, 28, 29)

Souring of figs (*yeast*) (30, 45)

Stigmatomycosis (*Nematospora spp*) (14, 15, 16, 17, 18, 19, 20, 22, 23, 24, 24a)

Dutch elm disease (*Ceratostomella ulmi*) (37, 38, 39, 40, 41, 42, 43)

Tree cricket canker of apple (*Leptosphaeria coniothyrium*) (1, 2)

"Yeast spot" of lima beans (*Nematospora phaseoli*) (23)

Potato scab (*Actinomyces scabies*) (31a)

Plum wilt (*Lasiodiplodia triflorae*) (43a)

Leaf spot of tomatoe (*Septoria lycopersici*) (31a)

HEMIPTERA

14 *Dysdercus cingulatus* (Fabricius)

15 *Dysdercus fasciatus* Signoret

16 *Dysdercus intermedius* Distant

17 *Dysdercus nigrofasciatus* Stål

18 *Dysdercus superstitiosus* (Fabr)

19 *Dysdercus spp*

20 *Leptoglossus balteatus* (L)

21 *Leptoglossus zonatus* (Dall)

22 *Phthia picta* (Drury)

23 *Nezara hilaris* Say

24 *Nezara viridula* L

24a *Antestia lineaticollis* (Stål)

HOMOPTERA

25 *Aphis gossypii* Glov

26 *Schizoneura lanigera* Hausmann

27 *Aleyrodes citri* R and H

28 *Ceroplastes floridensis* Comstock

29 *Dactylodius citri* Risso

COLEOPTERA

30 *Carpophilus hemipterus* L

31 *Carabidae* (species not known)

31a *Epitrix cucumeris* Harris

32 *Leptostylus macula* Say

33 *Leptura nitens* Forst = *Strophiona nitens* Forst

34 *Dendroctonus ponderosae* Hopk

34a *Dendroctonus piceaperda*

34b *Dendroctonus pseudosugae*

35 *Ips grandicollis* Eich

36 *Ips pini* Say

36a *Ips emarginatus* (Le C)

36b *Ips interger* (Eich)

36c *Ips oregoni* (Eich)

37 *Scolytus scolytus* Fabr

38 *Scolytus multistriatus* Marsh

39 *Scolytus sulcifrons* Rey

40 *Scolytus affinis* Eggers

41 *Scolytus laevis* Chapuis

TABLE I —SOME OF THE MORE IMPORTANT INSECT-TRANSMITTED PLANT
DISEASES AND THEIR RESPECTIVE INSECT VECTORS —*(Continued)*

Diseases	Vectors
	42 *Scolytus pygmaeus* Fabr
	42a *Scolytus sulcatus* Le C
	42b *Scolytus ventralis* Le C
	42c *Scolytus praeceps* Le C
	43 *Hylurgopinus rufipes* Eich
	LEPIDOPTERA
	43a *Aegeria exitosa* Say
	DIPTERA
	44 *Sciara thomae* L
	45 *Drosophila ampelophila* Leow
	46 *Hylemyia brassicae* Bouche
	HYMENOPTERA
	47 *Blastophaga psenes* L
	48 Bees
Protozoan diseases	**HEMIPTERA**
Flagellosis of laticiferous plants	1 *Dieuches humilis* Reut
Leptomonas davidi (1, 3, 6)	2 *Lygaeus kalmii* Stål
Herpetomonas elmassiani (4)	3 *Nysius euphorbiae* Horvath
Herpetomonas lygaeorum (2)	4 *Oncopeltus fasciatus* Dallas
Phytomonas leptovasorum (5)	5 *Lincus securiger* (Breddin)
	6 *Stenocephalus agilis* Scopoli

TABLE II —SOME OF THE MORE IMPORTANT VECTORS OF PLANT DISEASES
AND THE DISEASES THAT THEY TRANSMIT

Vectors	Diseases
ORTHOPTERA	1 Tree-cricket canker of apple
Gryllidae	(*Leptosphaeria coniothyrium*)
Oecanthus niveus De G (1)*	2 Potato spindle tuber (Solanum
Oecanthus angustipennis Fitch	virus 12)
(1)	3 Potato unmottled curly dwarf
Locustidae	(Solanum virus 13)
Chortophaga viridifasciata var	4 Cotton wilt (*Fusarium vasin-*
austratior De G (4)	*fectum*)
Dissosteira carolina L (4)	
Encoptolophus texensis Brun (4)	
Melanoplus differentialis	
Thomas (4)	
Melanoplus femur-rubrum De G	
(4)	
Melanoplus mexicanus Sauss	
(4)	
Melanoplus spp (2, 3)	

* The numbers in parentheses following the name of the vector refer to the numbers of
the diseases transmitted as given in the opposite column

Table II —Some of the More Important Vectors of Plant Diseases and the Diseases That They Transmit —*(Continued)*

Vectors

Diseases

Schistocerca americana Drury
(4)

Schistocerca obscura Fabr (4)
Spharagemon cristatum Scudd
(4)

Tomonotus aztecus Sauss (4)
Trimerotropsis citrina Scudd
(4)

THYSANOPTERA
Thripidae
Franklimella lycopersici Andr
(2)
Franklimella moultoni Hood (2)
Franklimella occidentalis Perg
(2)
Heliothrips femoralis Reut (3)
Thrips tabaci Lind (1, 2)

1 Pineapple yellow spot (Ananas virus 1)
2 Tomato spotted wilt (Lycopersicum virus 3)
3 Bean bacteriosis *(Phytomonas medicaginis* var *phaseolicola)*

HEMIPTERA
Lygaeidae
Dieuches humilis Reut (1a)
Lygaeus kalmii Stål (1c)
Nysius euphorbiae Horvath (1a)
Oncopeltus fasciatus Dallas (1b)
Miridae
Adelphocoris rapidus (Say) (5)
Campylomma verbasci (Meyer)
(5)
Lygus pratensis L (2, 3, 4, 5, 6)
Orthotylus flavosparsus (Sahlb)
(5)
Plagiognathus politus Uhl (5)
Poeciloscytus basilis Reut (5)
Tingidae
Piesma cinerea (Say) (7)
Piesma quadrata Fieb (6a)
Coreidae
Anasa tristis De G (8)
Dysdercus cingulatus (Fabr) (9)
Dysdercus fasciatus Signaret (9)
Dysdercus intermedius Distant
(9)
Dysdercus nigrofasciatus Stål (9)

1 Flagellosis of lacticiferous plants
  a *Leptomonas davidi*
  b *Herpetomonas elmassiani*
  c *Herpetomonas lygaeorum*
2 Potato spindle tuber (Solanum virus 12)
3 Potato unmottled curly dwarf (Solanum virus 13)
4 A virus disease of rape and rutabaga
5 Fire blight *(Erwinia amylovora)*
6 Leaf curl of sugar beet (Beta virus 3)
6a Rape savoy
7 Savoy of sugar beet (Beta virus 5)
8 Anasa wilt of cucurbits
9 Stigmatomycosis *(Nematospora spp)*
10 Inspissosis of citrus fruits *(Nematospora coryli)*
11 "Yeast spot" of lima beans *(Nematospora phaseoli* Wingard)

TABLE II —SOME OF THE MORE IMPORTANT VECTORS OF PLANT DISEASES
AND THE DISEASES THAT THEY TRANSMIT —*(Continued)*

Vectors

Diseases

Dysdercus superstitiosus (Fabr)
(9)

Antestia lineaticollis Stal   (9)

Dysdercus spp (9)

Leptoglossus bolteatus (Linne) (9)

Leptoglossus zonatus (Dall) (10)

Phthia picta (Drury) (9)

Stenocephalus agilis Scopoli (1a)

Pentatomidae

Lincus spathuliger (Breddin)
(12)

Nezara hilaris Say (11)

Nezara viridula L (9, 10)

12 Phloem necrosis of coffee
(*Phytomonas leptovasorum*)

HOMOPTERA

Cicadellidae

Aceratagallia sanguinolenta (Provancher (11)

Cicadulina (Balclutha) mbila Naude (8, 13)

Cicadulina storeyi China (8, 13)

Cicadulina zeae China (8, 13)

Deltocephalus dorsalis Motsch (12)

Empoasca fabae Harris (1)

Empoasca mali Le Baron (14)

Euscelis exitiosus (Uhl) (10)

Euscelis striatulus Fall   (4)

Eutettix tenellus Baker (5)

Macrosteles divisus (Uhl) (2)

Macropsis trimaculata Fitch (7, 9)

Nephotettix apicalis var *cincticeps* Motsch (12)

Thamnotettix geminatus V an D (2)

Thamnotettix montanus Van D (2)

Fulgoridae

Delphacinae

Delphacodes striatella Fall (*Liburnia striatella* Fall)
(15)

Peregrinus maidis Ashm (3)

1 Hopper burn of potato and other plants

2 Aster yellows (Callistephus viruses 1 and 1A)

3 Corn mosaic (Zea virus 1)

4 Cranberry false blossom (Vaccinium virus 1)

5 Curly top of sugar beet (Beta virus 1)

6 Fiji disease of sugar cane (Saccharum virus 2)

7 Little peach (Prunus virus 1A)

8 Mottle of corn (Zea virus 3)

9 Peach yellows (Prunus virus 1)

10 Potato unmottled curly dwarf (Solanum virus 13)

11 Potato yellow dwarf (Solanum virus 16)

12 Rice dwarf (Oryza virus 1)

13 Streak of corn (Zea virus 2)

14 Fire blight (*Erwinia amylovora*)

15 Stripe of rice (Oryza virus 2)

16 Psyllid yellows of potato

17 Bacterial gall of Douglas fir (*Bacterium pseudotsugae*)

18 Abacá bunchy top (Musa virus 2)

TABLE II —SOME OF THE MORE IMPORTANT VECTORS OF PLANT DISEASES AND THE DISEASES THAT THEY TRANSMIT —(*Continued*)

Vectors

Perkinsiella saccharicida Kirk (6)

Perkinsiella vastatrix Breddin (6)

Chermidae

Chermes cooleyi Gill (17)

Paratrioza cockerelli Sulc (16)

Aphididae

Amphorophora rubicola (Oestlund) (50, 51)

Amphorophora rubi Kalt (50, 51, 63)

Amphorophora sensoriata Mason (50, 51)

Anuraphis padi L (*Aphis pruni*) (39)

Anuraphis tulipae B de Fonsc (60)

Aphis apigraveolens Theob (28)

Aphis avenae Fabi (65)

Aphis convolvuli Kalt (34)

Aphis forbesi Weed (54)

Aphis gossypii Glov (23, 28, 29, 31, 63, 64, 74, 78)

Aphis graveolens Essig (28)

Aphis laburni Kalt (*Aphis leguminosae* Theo) (40)

Aphis maidis Fitch (58, 63)

Aphis medicaginis Koch (23)

Aphis middletonii Thomas (28)

Aphis pomi De G (63, 65)

Aphis rhamni abbreviata Patch (43)

Aphis rubicola Oestl (*rubiphila* Patch) (49)

Aphis rumicis L (23, 25, 30, 42, 57, 62, 63, 70)

Aphis spiraecola Patch (23)

Brevicoryne brassicae L (23, 28, 38, 52, 61, 63)

Capitophorus fragaefolii Ckl (53, 55, 56)

Capitophorus tetrarhodus (Walker) (26)

Diseases

19 Alfalfa mosaic (Medicago viruses 1 and 2)

20 Aucuba mosaic of potato (Solanum virus 9)

21 Banana bunchy top (Musa virus 1)

22 Banana mosaic (Musa virus 3)

23 Bean mosaic (Phaseolus virus 1)

24 Bean yellow mosaic (Phaseolus virus 2)

25 Beet mosaic (Beta virus 2)

26 Blackberry dwarf (Rubus virus 5)

27 Cabbage ring spot (Brassica virus 1)

28 Cauliflower mosaic (Brassica virus 3)

29 Celery calico (Apium virus 2)

30 Common mosaic of pea (Pisum viruses 2 and 2C)

31 Cucumber mosaic (Cucumis virus 1)

32 Dahlia mosaic (Dahlia virus 1)

33 Enation mosaic of pea (Pisum virus 1)

34 Freesia mosaic (Freesia virus 1)

35 Henbane mosaic (Hyoscyamus virus 1)

36 Iris mosaic (Iris virus 1)

37 Lettuce mosaic (Lactuca virus 1)

38 Mosaic of crucifers (Brassica virus 4)

39 Peach mosaic (Prunus virus 5)

40 Peanut rosette (Arachis virus 1)

41 Pelargonium leaf curl (Pelargonium virus 1)

42 Potato leaf roll (Solanum virus 14)

TABLE II—SOME OF THE MORE IMPORTANT VECTORS OF PLANT DISEASES
AND THE DISEASES THAT THEY TRANSMIT —(*Continued*)

Vectors	Diseases
Cavariella capreae Fabr (28)	43 Potato mosaic (Solanum virus 3)
Hyalopterus atriplicis (L) (23, 65)	44 Potato spindle tuber (Solanum virus 12)
Hysteroneura setariae Thomas (58, 63)	45 Potato streak (leaf drop) Solanum viruses 2 and 3)
Macrosiphum ambrosiae (Thomas) (23)	46 Potato tuber blotch (Solanum virus 8)
Macrosiphum gei Koch (solanifolii Ashm) (23, 24, 25, 30, 31, 36, 44, 47, 59, 60, 63)	47 Potato unmottled curly dwarf (Solanum virus 13)
Macrosiphum pelargonii Kalt (41, 60)	48 Potato yellow dwarf (Solanum virus 16)
Macrosiphum (*Illinoia*) *pisi* (Kalt) (19, 23, 24, 30, 33, 62, 63)	49 Raspberry leaf curl (Rubus viruses 3 and 3A)
Macrosiphum sonchi L (37)	50 Raspberry yellow mosaic (Rubus virus 2)
Myzus circumflexus Buckt (28, 31, 42, 59)	51 Red-raspberry mosaic (Rubus virus 1)
Myzus persicae Sulz (20, 23, 27, 28, 30, 31, 32, 35, 36, 37, 38, 42, 44, 45, 46, 47, 48, 52, 57, 60, 63, 70)	52 Stock mosaic (Matthiola virus 1)
	53 Strawberry crinkle (Fragaria virus 2)
Myzus pseudosolani Theob (31, 42, 59)	54 Strawberry dwarf (Fragaria virus 4)
Pentalonia nigronervosa Coq (18, 21, 22)	55 Strawberry witchs'-broom (Fragaria virus 3)
Rhopalosiphum melliferum Hottes (28)	56 Strawberry xanthosis (Fragaria virus 1)
Rhopalosiphum prunifoliae Fitch (63)	57 Sugar-beet yellows (Beta virus 4)
Rhopalosiphum pseudobrassicae Davis (23, 28, 52, 63)	58 Sugar-cane mosaic (Saccharum virus 1)
Schizoneura lanigera Hausman (66, 67, 68)	59 Tobacco mosaic (Nicotiana virus 1)
Aleyrodidae	60 Tulip mosaic (Tulipa virus 1)
Aleyrodes citri R and H (74)	61 Turnip mosaic (Brassica virus 2)
Bemisia gossypiperda var *mosaicurectura* Ghesq (71)	62 White-clover mosaic (Trifolium virus 1)
Bemisia nigeriensis Corb (71)	63 Yellow dwarf of onion (Allium virus 1)
Bemisia gossypiperda Misra and Lamba (72, 73)	64 Yellow flat of lily (Lilium virus 1)
Coccidae	
Pseudococcus brevipes (Ckl) (75, 76)	

TABLE II —SOME OF THE MORE IMPORTANT VECTORS OF PLANT DISEASES
AND THE DISEASES THAT THEY TRANSMIT —(*Continued*)

Vectors

Ceroplastes floridinsis Comstock
(74)
Dactylodius citri Risso (74)
Lecanium corni Bouche (77)

Diseases

65 Fire blight (*Erwinia amylovora*)
66 Canker of apple (*Diplodia griffoni*)
67 European canker (*Nectria galligena*)
68 Perennial canker of apple (*Gloeosporium perennans*)
70 Sugar-beet mosaic (Beta virus 2)
71 Cassava mosaic (Manihot virus 1)
72 Leaf curl of cotton (Gossypium virus 1)
73 Leaf curl of tobacco (Nicotiana virus 10)
74 Sooty mold of orange (*Capnodium citri*)
75 Green spotting of pineapple
76 Mealy-bug wilt of pineapple
77 Grape mosaic (Vitis virus 1)
78 Abacá mosaic
79 Froghopper blight of sugar

COLEOPTERA

Nitidulidae
Carpophilus hemipterus L (1, 2)
Coccinellidae
Hippodamia convergens Guer
(3)
Carabidae
Unidentified species (4)
Scarabaeidae
Phyllophaga sp (5)
Cerambycidae
Leptostylus macula Say =
Astylopsis macula (Say) (6)
Leptura nitens Forst = *Strophiona nitens* (Forst) (6)
Chrysomelidae
Chaetocnema denticulata Ill (5)
Chaetocnema pulicaria Melsh
(5)

1 Souring of figs (yeast)
2 Smut of figs (*Aspergillus niger*)
3 Fire blight (*Erwinia amylovora*)
4 Ergot of cereals and grasses (*Claviceps paspali*)
5 Bacterial wilt of corn (*Phytomonas stewarti*)
6 Chestnut blight (*Endothia parasitica*)
7 Cucumber mosaic (Cucumis virus 1)
8 Potato spindle tuber (Solanum virus 12)
9 Potato unmottled curly dwarf (Solanum virus 13)
10 Bacterial wilt of cucurbits (*Erwinia tracheiphila*)
11 Bacterial wilt of Solanaceae (*Erwinia solanacearum*)

TABLE II —SOME OF THE MORE IMPORTANT VECTORS OF PLANT DISEASES
AND THE DISEASES THAT THEY TRANSMIT —*(Continued)*

Vectors

Diabrotica   duodecimpunctata
Oliv (5, 7, 10)

Diabrotica longicornis Say (5)

Diabrotica soror Le C (3)

Diabrotica vittata Fab (7, 10)

Disonycha   triangularis   (Say)
(8)

Epitrix cucumeris Harris (8, 9,
15, 20)

Leptinotarsa   decimlineata Say
(8, 9, 11)

Orsodacne atta (Ahr) (3)

Systena taeniata (Say) (8, 9)

Dermistidae

Attagenus piceus Oliv (3)

Anthrenus sp (3)

Glischrochielus   fasciatus   Oliv
(3)

Curculionidae

Cryptorrhynchus lapathi L (12)

Elateridae

Melanotus oregonensis (Le C)
(3)

Scolytidae

Dendroctonus ponderosae Hopk
(13)

Dendroctonus piceaperda   (18)

Dendroctonus pseudotsugae (19)

Ips   grandicollis   Eich   (13)

Ips interger Eich (13)

Ips pini Say (13)

Ips emarginatus (Le C)   (13)

Ips oregoni (Eich) (13)

Scolytus   rugulosis   Ratz   (3)

Scolytus scolytus Fabr (14)

Scolytus multistriatus Marsh (14)

Scolytus   sulcifrons   Rey   (14)

Scolytus   affinis   Eggers   (14)

Scolytus laevis Chapius (14)

Scolytus pygmaeus Fabr (14)

Scolytus sulcatus Le C (14)

Scolytus ventralis Le C (16)

Scolytus praeceps Le C (17)

Scolytus subscaber Le C (17)

Diseases

12 Bacterial disease of willows
[*Pseudomonas   (Phytomonas)
saliciperda*]

13 Blue stain of coniferous trees
(*Graphium spp , Ceratostomella
spp*)

14 The Dutch elm disease [*Cera-
tostomella ulmi* (Schw) Buis-
man]

15 Potato   scab   (*Actinomyces
scabies*)

16 Brown   stain   of   white   fir
(*Trichosporium symbioticum*)

17 Brown   stain   of   white   fir
(*Spicaria anomala*)

18 Blue stain of spruce (*Cerato-
stomella piceaperda*)

19 Blue   stain   of   Douglas   fir
(*Ceratostomella pseudotsugae*)

20 Tomato   leaf   spot   (*Septoria
lycopersici*)

TABLE II —SOME OF THE MORE IMPORTANT VECTORS OF PLANT DISEASES
AND THE DISEASES THAT THEY TRANSMIT —*(Continued)*

Vectors	Diseases
LEPIDOPTERA	1 Bacteriosis of prickly pear plants (*Erwinia cacticida*)
Pyralididae	2 Fire blight (*Erwinia amylovora*)
Mimorista flavidissimalis Grote (1)	3 Black rot of crucifers (*Phytomonas campestris*)
Phycitidae	4 Plum wilt (*Lasiodiplodia triflorae*)
Cactoblastis bucyrus Dyar (1)	
Cactoblastis cactorum Berg (1)	
Melitara prodenialis Walker (1)	
Melitara junctelinsella Hulst (1)	
Aegeriidae	
Aegeria exitosa Say (4)	
Olethreutidae	
Carpocapsa pomonella L (2)	
Papilionidae	
Plusia brassicae Riley (3)	
DIPTERA	1 Ergot of cereals and grasses (*Claviceps paspali*)
Mycetophilidae	2 Fire blight (*Erwinia amylovora*)
Sciara thomae L (1)	3 Olive knot (*Erwinia savastanoi*)
Bibionidae	4 Bacterial rot of apples (*Phytomonas melophthora*)
Bibio albipennis Say (2)	5 The heart rot of celery (*Erwinia carotovora*)
Trypetidae	6 Souring of figs (yeast)
Dacus oleae Rossi (3)	7 Smut of figs (*Aspergillus niger*)
Rhagoletis pomonella Walsh (4)	8 Blackleg of cabbage (*Phoma lingam*)
Drosophilidae	9 Potato blackleg (*Erwinia carotovora*)
Drosophila ampelophila Leow (6, 7)	10 Soft rot of crucifers (*Erwinia carotovora*)
Drosophila funebris Fabr (2)	
Elachiptera costata Leow (5)	
Scaptomyza graminum Fall (5)	
Anthomyiidae	
Hylemyia antiqua Meig (2)	
Hylemyia brassicae Bouché (8, 10)	
Hylemyia ciliciura Rond (9)	
Hylemyia lipsia Walker (2)	
Hylemyia trichodactyla Rond (9)	
Pegomyia calyptrata Zett (2)	
Calliophoridae	
Cynomyia cadaverina Desv (2)	
Muscidae	
Musca domestica L (2)	
Muscina assimilis Fall (2)	
Muscina stabulans Fall (2)	

TABLE II —SOME OF THE MORE IMPORTANT VECTORS OF PLANT DISEASES
AND THE DISEASES THAT THEY TRANSMIT —(*Continued*)

Vectors

Diseases

HYMENOPTERA
  Chalcididae
    Blastophaga psenes L (1)
  Formicidae
    Formica fusca L var subserica
      Say (2)
    Formica pallidefulva Latr subsp
      schaufussi Mayr (2)
    Lasius niger (L) var *ameri-
      canus* Emerv (2)
    Prenolepis imparis Say (2)
  Vespidae
    Polistes sp (2)
    Vespula sp (2)
  Apidae
    Bees (3)

1 Endosepsis of figs (*Fusarium
   moniliforme* var *fici*)
2 Fire blight (*Erwinia amyl-
   ovora*)
3 Downy mildew of lima beans
   (*Phytophthora phaseoli*)

ACARINA (MITES)
    Eriophyes ribis (Westw) Nal (1)
    Pediculopsis graminum Reut (2)

1 Reversion of currants (Ribes
   virus 1)
2 Silver top of June grass and
   bud rot of carnation (*Sporo-
   trichum poae*)

SLUGS
    Agriolimax agrestis L (1)
NEMATODES
    Aphelenchus avenae Bost (6)
    Anguillulina dipsaci Kuhn (2)
    *Anguillulina   similis   * (Cobb)
      Goodey (5)
    Heterodera schactii (3)
    Tylenchus multicinta Cob (6)
    Tylenchus pratensis de Man (4) (6)
    *Tylenchus   tritici   * (Steinbuch)
      Bastian (1)

1 Black rot of crucifers (*Phyto-
   monas campestris*)
1 Dilophospora disease of ce-
   reals
2 Potato tuber rot
3 "Potato sickness" (*Colleto-
   trichum atromentarium*)
4 Root rot of cereals
5 Root rot of sugar cane
6 Soft rot (*Erwinia carotovora*)

BIRDS
    Certhia   familiaris   americana
      (Bonap) (1)
    Dryobates   pubescens   medianus
      (Swainson) (1)
    Junco hyemalis L (1)
    Mniotilta varia L (1)
    Regulus satrapa Licht (1)
    Sitta carolinensis Lath (1)
    Sphyrapicus varius L (1)

1 Chestnut blight (*Endothia
   parasitica*)

TABLE III—A COMPARISON OF CERTAIN REPRESENTATIVE FUNGUS DISEASES OF PLANTS IN RESPECT TO TRANSMISSION PHENOMENA

Disease	Pathogen	Known insect vectors	Nature of insect transmission	Is vector obligatory in nature?	Does pathogen hibernate in vector?	Congenital transmission in vector?
Ergot of cereals	*Claviceps purpurea*	Many species of flies	Mechanical dissemination without wounding	No	No positive evidence	No
Blue stain of conifers	*Ceratostomella ips C spp Tuberculariella ips* and other fungi	*Ips pini I grandicollis* and other bark beetles	Mechanical dissemination with wounding	Yes	Yes	No
Dutch elm disease	*Ceratostomella ulmi*	*Scolytus scolytus S multistriatus S sulcifrons S affinis S pygamaens,* and *Hylurgopinus rufipes*	Mechanical dissemination with wounding	Yes	Yes	No
Endosepsis of figs	*Fusarium moniliforme* var *fici*	*Blastophaga psenes*	Mechanical dissemination without wounding	Yes	No	No
Souring of figs	Two or more unnamed species of yeast	*Carpophilus hemipterus, Drosophila ampelophila* and several species of thrips	Mechanical dissemination with and without wounding	No but development is largely dependent upon the vectors	No	No
Fig smut	*Aspergillus niger*	*Carpophilus hemipterus Drosophila ampelophila* and several species of thrips	Mechanical, dissemination with and without wounding	No, but development is largely dependent upon the vectors	No	No
Stigmatomycosis of cotton beans, citrus, and other plants	*Nematospora spp Spermophthora gossypii,* and *Eremothecium cymbalariae*	*Dysdercus spp Nezara hilaris,* and other plant bugs	Biological?	Yes	Not known	Not known
Perennial canker of apple	*Gleosporium perennans*	*Schizoneura lanigera*	Mechanical, wounding without dissemination	Yes	No	No
Downy mildew of lima beans	*Phytophthora phaseoli*	Bees	Mechanical dissemination without wounding	No	No	No
Tree cricket canker of apple and raspberry	*Leptosphaeria coniothyrium*	*Oecanthus niveus O angustipennis*	Mechanical dissemination with wounding	No	No	No

TABLE IV — COMPARISON OF CERTAIN REPRESENTATIVE VIRUS DISEASES OF PLANTS IN RESPECT TO TRANSMISSION PHENOMENA

Virosis	Known host range	Transmission by artificial sap inoculation	Longevity of extracted virus	Transmission through seed	Transmission through pollen	Known insect vectors	Nature of insect transmission	Congenital transmission in vector	Additional significant data	Incubation period in vector
Spindle tuber	Potatoes only	Yes, highly infectious	Less than 24 hours *in vitro* 7 days in dried leaves	No positive evidence	Not known	Many including aphids grass hoppers flea beetles, Colorado potato beetle the tarnished plant bug and others	Mechanical	No positive evidence		None
Yellow dwarf of onions	*Allium cepa, A saltvum, Narcissus tazetta N jonquilla*	Yes	112 hr	No	No	More than 50 species of aphid and other insects	Mechanical	No		None
Cucumber mosaic	Extensive many unrelated plants	Yes	2 to 5 days	Yes in small percentage	Not known	*Aphis gossypi Myzus persicae M solani M circumflexus Macrosiphum gei* and *Dia bratica vitata*	Mechanical and probably also biological by certain species of aphid (Hogan 1930)	No		None
Potato leaf roll	Potato, tomato, *Solanum villosum S dulcamara Datura stramonium* and *D tatula*	No	Not known	No positive evidence	Not known	*Myzus persicae, M pseudosolani, M circumflexus* conflicting evidence regarding several other nonrelated species	Probably only biological	No positive evidence		Minimum of 54 hr in *Myzus persicae*
Aster yellows	Extremely wide including species in more than 30 families	No	Not known	No	No	*Macrosteles divisa Thamnotettix montanus T garmanatus*	Biological	No		10 days
Curly top of sugar beet	Extremely wide	With difficulty in small percentage of trials	Less than 72 hr exposed to air, as long as 100 days under anaerobic conditions	No	No	*Eutettix tenellus*	Biological	No		Minimum of 7 hr with single insect 20 min with 50 or more insects
Peach yellows	Peach, wild plums (*Prunus myobalan P munsoniana*) Japanese plum (*P salicina*)	No	Not known	No	No	*Macropsis trim aculata*	Biological	Not known		8 to 26 days

Disease	Host range		Persistence			Vector	Transmission			Incubation
Dwarf disease of rice	Rice wheat rye, oats, and several wild grasses	No	Not known	No	No	*Nephotettix apicalis* var *cincticeps* and *Deltocephalis dorsalis*	Biological	Yes	Adults cannot acquire the virus by feeding They may transmit the virus but must acquire it in the larval stage	An incubation period required but minimum time not established
Spotted wilt	Very wide	Yes	3 hr	No	No	*Thrips tabaci* and *Frankliniella lycopersica*	Biological	No	Adults cannot acquire the virus by feeding They may transmit the virus but must acquire it in the larval stage	5 to 7 days
Yellow spot of pineapple	Pineapple and a few weeds chiefly *Emilia sagitata*	Yes, but with difficulty	Not known	Not known	Not known	*Thrips tabaci*	Biological	No	Transmitted by adults only	
Crinkle leaf of sugar beet	Sugar beets, red beets man golds spinach, and *Rumex acetosa*	Yes with difficulty 13°C of trials	Not known	No	No	*Piesma quadrata* Fieb	Apparently biological	No		Variable not definitely known
Leaf curl of cotton	Cotton and several species of *Hibiscus*	No	Not known	No	No	*Bemisia gossypiperda*	Apparently biological	No		Not more than 30 min
Latent (X) virus of potato	Potato tobacco and several other solanaceous plants	Yes	6 weeks or longer	No	No	None				
Tobacco mosaic	Tobacco and many other solanaceous and nonsolanaceous plants	Yes readily	3 months to 3 years or more, very resistant	No	No	*Myzus persicae* M *pseudosolani Macrosiphum gei* with difficulty and to certain hosts only	Probably mechanical in most cases though selective transmission on various hosts suggests a possible biological relationship	No	This virus has been isolated in the form of a pure protein crystals and many physical and chemical properties determined	None
Wheat mosaic	Wheat and rye	Yes	Not known	No	No	None known		No	Infection in nature only underground through either roots or crown Aerial spread absent	

TABLE V —A COMPARISON OF CERTAIN REPRESENTATIVE BACTERIAL
DISEASES OF PLANTS IN RESPECT TO TRANSMISSION PHENOMENA

Disease	Pathogen	Known insect vectors	Nature of insect transmission	Is vector obligatory in nature?	Does pathogen hibernate in vector?	Congenital transmission in vector?
Fire blight	*Erwinia amylovora*	Bees wasps, flies and many sucking insects	Mechanical dissemination with and without wounding	No	No	No
Cucurbit wilt	*Erwinia tracheiphila*	*Diabrotica vittata* and *D 12 punctata*	Biological dissemination with wounding	Yes	Yes	No
Soft rot of plants	*Erwinia carotovora*	*Hylemyia cilicrura H brassicae* and other dipterous insects	Biological dissemination with wounding	No	Yes	No
Olive knot	*Erwinia savastanoi*	*Dacus oleae*	Biological dissemination with wounding	No	Yes	Yes
Wilt of corn	*Phytomonas stewarti*	*Chaetocnema pulicaria C denticulata, Diabrotica longicornis, Hylemyia cilicrura*	Biological, dissemination with wounding	No but development is largely dependent upon the vectors	Yes	No evidence
Apple rot	*Phytomonas melophthora*	*Rhagoletis pomonella*	Biological dissemination with wounding	Yes	No positive evidence	No

TABLE VI.—A COMPARISON OF CERTAIN REPRESENTATIVE DISEASES OF ANIMALS IN RESPECT TO TRANSMISSION PHENOMENA

Disease	Pathogen	Arthropod vector	Definitive host	Intermediate host	Method of transmission	Incubation period in vector	Congenital transmission in vector?
Filariasis (elephantiasis)	Filaria bancrofti	Several species of mosquito	Man	Mosquitoes several different species	Contaminative following feeding of infective mosquito	16 to 25 days	No
Texas fever	Babesia bigema	Cattle ticks, Boophilus annulatus, B spp and Ixodes ricinus	Cattle ticks, Boophilus annulatus, B spp, and Ixodes ricinus	Cattle	Inoculative by bite of the ticks	One complete generation of the vector	Yes the disease is transmitted only by the progeny of ticks that feed on infected cattle
Rocky Mountain spotted fever	Dermacentroxenus (Rickettsia) rickettsii	The tick (Dermacentor andersoni)	?	?	Inoculative by bite of infective tick (Dermacentor andersoni)	At least 9 days	Yes
The nagana disease of cattle	Trypanosoma brucei	The tsetse fly (Glossina morsitans)	The tsetse fly (Glossina morsitans)	Cattle	Inoculative by the bite of the tsetse fly	10 days	No
Sleeping sickness of man	Trypanosoma gambiense	The tsetse flies (Glossina palpalis and G tachinoides)	The tsetse flies (Glossina palpalis and G tachinoides)	Man	Inoculative by the bite of the tsetse flies	20–30 days	No
Malaria	Plasmodium vivax, P malariae and P falciparum	The anopheles mosquitoes	The anopheles mosquitoes	Man	Inoculative, by the bite of the mosquito	8–14 days	No
Yellow fever	A virus	Aedes aegypti and several other species of mosquito	?	Man and monkeys	Inoculative by the bite of the mosquito	9–14 days	No
Dengue	A virus	Aedes aegypti A albopictus and other mosquitoes	?	Man and monkeys	Inoculative by the bite of the mosquito	8–11 days	No
Bubonic plague	Pasteurella pestis	Xenopsylla cheopis and other species of insects	?	?	Inoculative by bite of flea and contaminative in excreta of flea	None	No
Typhus fever	Rickettsia prowazeki	The body louse (Pediculus humanus)	?	?	Inoculative by bite of louse or contaminative in excreta of louse	8–9 days	No
Trench fever	Rickettsia quintana	The body louse (Pediculus humanus)	?	?	Inoculative by bite of louse or contaminative in excreta of louse	5–9 days	No
Typhoid fever	Eberthella typhosa	Musca domestica and related species	?	?	Contaminative, both internally and externally	None	No

GLOSSARY

The author appreciates the difficulty of accurately defining any biological concept. Definitions, however, do aid in straight thinking, and failure to define terms often leads to confusion. Phytopathology and entomology are young sciences, and their terminologies are in the process of evolution. Consequently, so many of the terms have been used so loosely that some degree of definition is necessary if confusion is to be avoided.

Moreover, the sciences of phytopathology and entomology have developed their own distinctive terminologies which are not always clearly understood by specialists in the other field. The definitions given here are not intended to be invulnerable, and some people may object to the sense in which certain terms have been used. The definitions are included in the belief that they may be of assistance to some of the readers of this book.

Anemophilous Wind-pollinated

Antagonistic symbiosis Symbiosis in which one member of the association benefits at the expense of the other. Parasitism

Antibiosis An association between two or more organisms that is detrimental to one or more of them

Arthropod An organism with annulate body and segmented appendages, of Phylum Arthropoda which includes insects, mites, spiders, crustacea, centipedes, etc

Ascospores Sexually produced fungus spores borne in a special cell known as an "ascus "

Autocatalytic Stimulating a chemical reaction that results in the production of more of the stimulating substance

Autogenetic Pertaining to the spontaneous origin of living organisms

Basement membrane A thin noncellular layer constituting the internal limits of the epidermis of insects

Basipetally Successively from the apex to the base

Bromatia The peculiar enlarged ends of the mycelium of fungi cultivated by ants

Buccal cavity The foremost part of the stomodaeum lying just inside the mouth

Bursa copulatrix A modification of the vagina serving as a copulatory pouch

Caecum (*pl* caeca) An evaginated blind sac opening into the intestinal tract

Callus Soft parenchymatous tissue of cambial origin formed over a wound

Carrier In medicine, a person who is a constant host for an infectious pathogen but manifests no clinical symptoms of the disease. In plant pathology, a plant that contains a virus but develops no symptoms of a

virus disease   In earlier literature, "carrier" was used to designate an insect that transmitted a virus, but the term "vector" is now preferred

Cecidium   A plant gall

Chlamydospore   A thick-walled spore developed directly from hyphal cells and not borne on special sporophores

Chlorosis   A diseased condition characterized by a deficiency of cholorophyll

Chlorotic   Possessing less than the normal amount of chlorophyll

Chorion   The egg shell

Close pollination   The transference of pollen from the stamen of one flower to the stigma of another flower of the same plant

Clypeus   The facial area of the cranium of insects lying just above the labrum

Colleterial glands   Female accessory glands that secrete an adhesive substance used to fasten eggs to some sort of support

Colon   The posterior part of the hind-intestine, between the ileum and the rectum

Commensalism   Symbiosis in which neither party is injured or benefited or in which one member of the association is benefited without either benefit or injury to the other

Congenital transmission   Transmission from one generation to the next successive generation through the process of reproduction

Conidium   A fungus spore produced asexually and exogenously

Contagious   Spread by contact

Contaminative   Being transmitted by surface contamination without wounding by the vector

Coprophilous   Growing on the dung of animals

Coremia   A fruiting structure of fungi consisting of a group of erect intertwined hyphae bearing conidia at their apex

Crop   An enlargement of the esophageal region of the stomodaeum, often serving as food reservoir

Cross-pollination   The transference of pollen from the anther of flowers on one plant to the stigma of flowers on another plant

Cuticle   A layer of cutin found on the outside of the outer walls of epidermal cells of plants

Cuticula   The outer noncellular layer of the body walls of insects

Cutin   A tough waxy substance secreted on the surface of epidermal cells of plants

Cyclical   Involving a sexual reproduction cycle

Definitive host   The host in which the sexual stage of a parasite is found

Diploidization   The bringing together, in the same mycelium, of nuclei of opposite sex

Dissemination   To scatter or diffuse   The transportation of inoculum from one location to another   Does not imply either inoculation, ingression, or infection (*cf* Transmission)

Diverticulum   A blind saclike offshoot from the alimentary canal or other organs

Ecdysis   Molting, the process of casting off the skin

Ectosymbiosis Symbiosis in which the microsymbiote develops on the outside of the body of the other symbiote

Endemic The regular occurrence of a disease of man with little variation in abundance

Endocuticula The inner layer of the cuticula, usually not heavily sclerotized

Endogenous Arising from within the generating structure

Endophylaxis Plant resistance to insects caused by internal physiological properties

Endosymbiosis Symbiosis in which the microsymbiote develops within the body of the other symbiote

Enphytotic The regular occurrence of a disease of plants in a given locality with little variation in abundance   Analogous to, but not synonomous with, endemic

Enteric Relating to the intestinal organs

Entomophily Pollination of flowering plants through the agency of insects

Enzootic The regular occurrence of a disease of animals with little variation in abundance

Epicuticula A very thin nonchitinous layer on the outer surface of the cuticula

Epidemic The occurrence of a disease of human beings in abundant and destructive proportions

Epidemiology The study of epidemics

Epidermis The outermost layer of cells on most plant organs before the development of periderm

Epipharynx One of the mouth parts of insects, attached to the inner surface of the labrum, probably an organ of taste

Epiphylaxis Plant resistance to insects caused by external morphological factors

Epiphyte A plant that lives upon another plant but derives no nourishment from it   A place parasite

Epiphytotic The occurrence of a disease of plants in abundant and destructive proportions   Analogous to, but not synonomous with, epidemic

Epithelium A layer of cells covering the surface or lining a cavity

Epizootic The occurrence of a disease of animals in abundant and destructive proportions

Esophagus The tubular portion of the stomodaeum between the pharynx and the crop

Evagination The protrusion of an inner surface toward the outside

Exfoliated Separated in a thin layer from the underlying tissue

Exocuticula The outer layer of the cuticula, the layer most commonly sclerotized

Exogenous Arising on the outside of the generating structure

Facultative parasite An organism normally living as a saprophyte but that can live as a parasite

Facultative saprophyte An organism normally living as a parasite but that can live as a saprophyte

Filter chamber A part of the alimentary canal in Homoptera in which the anterior end of the mesenteron and the beginning of the hind-intestine are bound together, providing a means for water and carbohydrate solutes to pass by diffusion into the hind-intestine without passing through the mesenteron

Flagellate Possessing one or more flagella, a protozoan belonging to the Mastigophora and characterized by having one or more flagella

Flagellosis A disease caused by flagellate protozoa

Follicle Egg chamber, a compartment of the egg tube that contains an oocyte

Galeae The outer lobes of the maxillae

Germarium The end chamber of an ovariole (or testicular tube) containing the primary oogonium (or spermatogonia)

Glabrous Having few or no trichomes

Glossae The two median lobes of the labium

Gravid Pregnant, ready to bear young

Guttation Loss of water by exudation through hydathodes

Hemolymph The clear watery liquid in the body cavity of insects and other invertebrates The "blood" of insects

Heterothallism That condition in which the fusion of two mycelia of different nuclear complement is necessary for sexual reproduction

Hibernation The act of surviving the winter usually in a dormant or quiescent condition

Homosexual Producing only one kind of gamete

Host An organism on or in which a parasite lives

Hydathodes Openings through the epidermis of leaves usually located near the terminal veinlets They have no guard cells and serve for water loss by guttation when relative humidity is high

Hymenium The fruiting surface of Ascomycetes or Basidiomycetes

Hyperplasia Overgrowth caused by increase in number of cells

Hypertrophy Overgrowth caused by increase in cell size

Hypodermis The epidermis of insects, the cell layer of the body wall of insects

Hypopharynx A tonguelike prolongation of the floor of the mouth of insects, attached to the inside wall of the labium

Hypopus A stage in the development of certain mites especially adapted for their dissemination by insects to whose bodies they cling by means of special organs of suction

Ileum The anterior part of the hind-intestine between the mesenteron and the colon

Imperfect stage (of a fungus) The stage that does not include spores formed as a result of a sexual process

Incubation period That time elapsing between the time of inoculation and infection (in reference to a plant pathogen) In general, the period of embryonic development The time elapsing between ingestion of an infectious agent by an insect and the time when the insect becomes infective

Infection That process in the development of a disease in which the pathogen becomes established on the suscept and begins to drive its nourishment from it

Infection court That portion of a suscept through which a pathogen may infect under suitable environmental conditions

Infectious Capable of being transmitted by inoculation

Infective Able to communicate infection An insect is said to be "infective" when, after ingesting an infectious agent, it is able to induce infection by feeding on the suscept The same as "viruliferous" when used in connection with virus diseases

Infestation To be present in large quantities in a given medium or locality

Infrabuccal pouch In ants, a spherical sac below the floor of the mouth and opening into the mouth

Ingression The act of gaining entrance into the tissues of the suscept Infection may or may not follow ingression Ingression may be accomplished by some pathogens without external aid Others require the aid of some wound-producing agent

Inoculation The act of placing inoculum on the infection court (or an assumed infection court) In medical science, the term usually implies insertion under the skin, thus including also the act of ingression, which is excluded in the sense used here

Inoculative Being transmitted through injection under the skin as by an insect vector

Inoculum Infective material, a pathogen or part of a pathogen that may infect and cause a disease

Instar The period or stage between molts in the metamorphosis of insects

Intermediate host reservoir Hosts in which a supply of the asexual stage of a parasite occurs

Invagination The retraction of a outer surface toward the inside

Invasion The spread of a pathogen through the tissues of a suscept

Isogamic Sexual reproduction by morphologically similar gametes

Kataplastic Overgrowths in which the new tissue is composed of undifferentiated elements

Klendusic Disease-escaping, having the property of klendusity

Klendusity The property of escaping infection under natural conditions although susceptible when inoculated artificially

Labella The sensitive spongelike organs at the end of the proboscis of certain Diptera, formed by a modification of the tip of the labium

Labium The lower tip of the insect mouth parts formed by the union of a second pair of maxillae

Labrum The upper lip of insects, covering the base of the mandibles and forming the roof of the mouth

Latent period The time elapsing between inoculation and the appearance of symptoms of the disease

Latex A viscid milky juice secreted by specialized cells of certain plants

Laticiferous Producing latex

Lesion A morphological or histological symptom of a disease

Longevity   Ability to live or survive for a long time

Macrogametocyte   The female sex cell arising from the merozoite of the malarial protozoan

Malpighian tubules   Long slender tubules opening into the alimentary tract of insects at the anterior end of the hind-intestine and having excretory functions

Mandibles   The first pair of appendages composing the mouth parts of insects   They assume various forms in different groups of insects

Maxillae (the first maxillae)   The second pair of appendages of the mouth parts of insects

Meristematic   Capable of producing new tissue by cell division

Merozoite   The third stage in the asexual development of the protozoan causing malaria

Mesenteron   The middle portion of the alimentary canal of insects which is of entodermal origin, the mid-intestine

Mesophyll   The chlorophyll parenchyma of leaves

Metamorphosis   Change of form, the progressive changes of form of an insect in growing from the egg through larva, pupa, to adult

Microgametocyte   The male sex cell arising from the merozoite of the malarial protozoan

Micropyle   A minute opening in the insect egg through which the spermatozoa enter in fertilization

Microsymbiote   A microorganism that lives in symbiosis with a more highly developed organism

Microtrichia   Nonarticulated hairs formed as extensions of the cuticula of insects

Mimetic   Imitative

Monophagous   Feeding on one plant or kind of food

Mutualism.   Mutualistic symbiosis

Mutualistic symbiosis   Symbiosis that is beneficial to both of the members of the association

Mycetocyte   A cell that harbors symbiotic microorganisms

Mycetome   A tissue composed of mycetocytes

Mycophagous   Feeding upon fungi

Necrosis   The death and destruction of cells or tissues

Necrotic   Characterized by rapid death and destruction of tissue

Oligophagous   Feeding on a limited number of plants or kinds of food

Oocyst   A resting nodular stage of the malarial parasite formed from the ookinete

Oocyte   The differentiated egg cell just before maturation

Oogonium   The first stage in the differentiation of the egg cell from the primary germ cell

Ookinete   The zygote of the malarial parasite

Ovaries   The mass of ovarian tubules in which the eggs are developed

Ovarioles   The egg tubes that together make up the ovary

Oviduct   One of the paired tubes through which the egg passes from the ovarian tubes into the vagina

Oviparous   Reproducing by eggs

Ovipositor The tubular organ of female insects by means of which eggs are deposited

Ovoviviparous Producing living young by the hatching of the egg while still in the body of the mother

Parasite An organism living in or on another living organism of a different species from which it derives all or part of its nourishment

Parasitism Living as a parasite

Parenchyma The thin-walled isodiametric cells of plant tissue

Parthenogenesis Reproduction by direct growth of egg cells without fertilization by the male element

Pathogen An organism that can cause a disease

Pathogenicity The ability of an organism to cause disease

Perfect stage (of a fungus) The stage that includes the spores formed as a result of a sexual process

Periderm A layer of cork cells on the outside of plant roots and stems and formed by growth of a cork cambium

Pharynx The back part of the mouth and the fore part of the esophagus

Physiologic race A biotype of group of closely related biotypes differing from other biotypes in physiological behavior

Phytocecidium A plant gall caused by the action of a plant

Phytophagous Feeding on plants

Phytotoxic Toxic to plants

Plasmodesma Delicate threads of protoplasm that pass through the walls between two cells, uniting the protoplasts of the two cells

Pleomorphism The inclusion of many different forms in the normal life cycle

Pollination The transference of pollen from the stamen to the stigma of flowers

Pollinia Masses of sticky pollen grains borne in packets and especially adapted to transportation by insects

Polyphagous Feeding on many different plants or kinds of food

Preservation Insurance of the survival of a pathogen by protecting it from unfavorable environmental conditions

Prestomal teeth Toothlike structures arising from the cleft between the labella lobes of the proboscis of certain Diptera

Primary infection First infection following a period of quiescence of a pathogen

Proboscis The extended or prolonged mouth parts of an insect

Proctodaeum The posterior part of the alimentary canal of insects which is of ectodermal origin, the hind-intestine

Prosoplastic Overgrowth in which new tissue is composed of well-differentiated elements

Protoplasmic membrane A semipermeable membrane consisting of the thin outer layer of the protoplasm of a cell

Protozoa Single-celled animals without true tissues or true organs

Proventriculus A specialized part of the fore-intestine immediately anterior to the ventriculus

Pseudotracheae False tracheae

Pseudovitellus   The mycetome of aphids

Pubescent   Having abundant trichomes

Pycnidium   A hollow multicellular fruiting body in which asexual spores are produced, characteristic of the Sphaeropsidales and certain Ascomycetes

Pycnium   A pycnidiumlike structure in the rusts in which are produced haploid spores that serve as agents of diploidization

Rectum   The posterior part of the hind-intestine, opening at the anus

Rickettsia   Minute bacterialike microorganisms that live symbiotically in the bodies of insects by which they often may be transmitted to higher animals on which they may become pathogenic

Roguing   The removal of plants because of disease or other undesired characters

Saprophyte   A plant that lives upon dead organic matter

Sclerotized   Infiltrated with a hard or tough substance

Secondary infection   Infection in a period of active spread of a disease

Self-pollination   The transference of pollen from the stamen to the stigma of the same flower

Setae   Hollow, pointed, articulated hairs formed by a modified epidermal cell

Setal sheath   A sheath surrounding the feeding puncture made in plant tissue by a homopterous insect, probably formed by the saliva of the insect reacting with the plant sap

Spermatheca   The reservoir in the female insect which receives the sperm during or shortly after copulation

Sporidium   Small spores produced on the basidia or promycelia of smuts and rusts

Sporozoites   Minute individuals produced by the oocyst of the malarial parasite   The form that invades the salivary glands of the mosquito

Stele   The axis or central cylinder of vascular plants consisting of the conducting tissues and associated supporting tissues

Stigma   The surface of the style of a flower through which the germinating pollen grain penetrates to reach the ovary

Stigmonose   A diseased condition resulting from localized injury caused by insect punctures

Stomata (*sing* stoma)   Specialized openings in the epidermis adapted for exchange of gases

Stomodaeum   The anterior part of the alimentary canal of insects which is of ectodermal origin, the fore-intestine

Stylets   Small slender sclerotized processes of the insect exoskeleton

Suscept   An organism that is susceptible to a given disease

Symbiote = Symbiont.   One partner of a symbiotic relationship   Commonly applied to a microorganism symbiotic with a more highly developed organism

Symbiosis   The condition of living together of two organisms of different species in close spatial relationship   Often used in a restricted sense implying mutualistic symbiosis

Teliospore   A spore of the Uredinales, usually a resting spore, that on germination produces a promycelium or a basidium

Thorax The second or intermediate region of the insect body, bearing the true legs and wings

Toxicogenic Capable of producing a toxic substance Insects that introduce a toxic substance into the plant while feeding are said to be "toxicogenic "

Toxiniferous Actively producing a toxic substance Toxicogenic insects may temporarily lose their ability to produce the toxic substance, in which case they would not be toxiniferous

Transmission The acts of disseminating and inoculating inclusively, the act of perpetuating a disease from one generation to another as through seed or vegetative propagation

There is some difference of opinion among plant pathologists in regard to the use of the phrase "disease transmission " Some maintain that a disease, not being a concrete body, cannot be transmitted, only the pathogen or infectious agent being subject to transmission The same objection is raised to the use of "disease dissemination " The author believes that these objections are not entirely valid and that there is ample justification, both etymological and traditional, for the use of either phrase However, from the standpoint of the phenomena of plant disease development, there appears to be some justification for not using the two terms interchangeably In this book, an effort has been made to use the term "dissemination" only in connection with the pathogen This restricted use is based on the concept that the pathogen may be *disseminated* widely but the disease is not *transmitted* until inoculation and infection have occurred Thus, an insect may *disseminate* a pathogen without *transmitting* the disease

Transpiration Loss of water by evaporation through stomata

Trichogen The modified epidermal cell of insects from which the setae arise

Trichomes Modified hairlike epidermal cells of plants

Vagina The egg passage formed by the union of the oviducts and through which the egg passes to the ovipositor

Vector An agent of dissemination or inoculation or both

Ventriculus The mesenteron, or mid-intestine

Viable Living or capable of growth

Virulence The degree of ability to produce disease A measure of pathogenicity

Viruliferous Capable of inducing a virus disease by feeding on the suscept Infective, in regard to virus diseases

Virus An ultramicroscopic, filterable, infectious agent

Vitellarium That part of the egg tube in which the oocytes grow to mature size

Wound cork Cork tissue formed in the process of healing a wound

Zoocecidium A plant gall caused by the action of an animal

Zygote An individual formed by the union of two gametes of opposite sex

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